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The genus *Lepiota* sensu stricto with observations on related taxa found in Colombia

Franco, Ana Esperanza, Ph.D.

City University of New York, 1994

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THE GENUS LEPIOTA SENSU STRICTO WITH OBSERVATIONS ON RELATED TAXA FOUND IN COLOMBIA

by

ANA ESPERANZA FRANCO

A dissertation submitted to the Graduate Faculty in Biology in partial fulfillment of the requirements for the degree of Doctor of Philosophy, The City University of New York.

1994

This manuscript has been read and accepted for the graduate Faculty in Biology in satisfaction of the dissertation requirements for the degree of Doctor of Philosophy.

1 OCT 1993
Date

Roy E. Halling
Chairman of Examining Committee
Dr. Roy E. Halling
The New York Botanical Garden

October 27, 1993
Date

Richard L. Chappell
Dr. Richard L. Chappell
Executive Officer

Thomas E. Jensen
Dr. Thomas E. Jensen
The City University of New York

Wm Wayt Thomas
Dr. Wm. Wayt Thomas
The New York Botanical Garden

Timothy J. Baroni
Dr. Timohy J. Baroni
State University College at Cortland

Gerald F. Bills
Dr. Gerald F. Bills
Merck Research Laboratories

Supervisory Committee

The City University of New York

ABSTRACT

The genus Lepiota sensu stricto with observations on related taxa found in Colombia

by

Ana Esperanza Franco

Advisor: Dr. Roy E. Halling

A preliminary taxonomic treatment of the species of Lepiota s.s. and related species that occur in Colombia is presented. The differences among genera are revised based on macro- and micro-morphology and chemical reactions. Descriptions of 29 species distributed among seven genera are provided. Line drawings of microscopic features for all species, photographs of basidiomata for 18 species, and SEM photomicrographs for three species supplement the descriptions.

Provisionally, thirteen new species are described and one new combination proposed. General information on distribution of the species, relationship with ants, phenoloxidases production and phylogeny is provided.

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CHAPTER I

INTRODUCTION

General Overview

The genus Lepiota (Pers.) S. F. Gray (Agaricaceae, Agaricales, Basidiomycotina) constitutes a large genus of white-spored agarics. These fungi play an important role in nutrient retention and recycling in tropical, subtropical and temperate regions Guzmán and Guzmán-Dávalos (1992). According to Guzmán and Guzmán-Dávalos (1992), the genus Lepiota s.l. is represented by more than 1700 names of which nearly 600 are synonyms, nomina nuda, doubtful species, or excluded species. Lepiota s.l. was split into 16 allied genera (Heinemann, 1973a; Singer, 1986) because of the increased value placed on microscopic features.

Although species of Lepiota are distributed worldwide, they predominantly occur in the tropics and subtropics (Patouillard, 1888; Pegler, 1972, 1983; Horak, 1980a; Guzmán and Guzmán-Dávalos, 1992; Guzmán-Dávalos and Guzmán, 1979, 1982; Singer, 1986) where the diversity decreases with altitude. However, considerable taxonomic work, including the first monographic treatment by

Candusso and Lanzoni (1990), has been completed for temperate representatives. Tropical accounts of Lepiota s.l. are available for Cuba (Berkeley and Curtis, 1869) where four new species from the island where described. Berkeley and Broome (1871) provided descriptions for a total of 68 species from Ceylon (Sri Lanka) based entirely on material received from two collectors, Thwaites and Gardner. Their accounts have played an important role as the nomenclatural base for tropical species of Lepiota. Many of their descriptions of agarics from the island have been transfered into Lepiota and related genera (Dennis, 1952, 1962; Singer, 1962; Pegler, 1972, 1977, 1983, 1986). Murrill (1911) cited 19 new species from Cuba, Jamaica and Mexico, and Beeli (1927, 1932, 1936) described over 40 species from the Congo. Dennis' (1952, 1962, 1970) treatments included about 45 lepiotas from Trinidad, British West Indies and Venezuela; over 20 of these were newly described. Heinemann (1969) cited eight species of Macrolepiota from the Congo, and later (Heinemann, 1973b, 1977) described nine new species of Leucoagaricus, and four new species of Leucocoprinus from Central Africa. In addition, he (Heinemann, 1979) described two new species of Leucoagaricus from Zaire. Pegler (1972) revised Lepiota from Sri Lanka using the Berkeley and Broome material. Pegler's (1977, 1983, 1986) floristic treatments cited 56 Lepiotas (five new) from Africa, 47 (10 new) from the Lesser Antilles, and 36 lepiotas from Sri Lanka, 32 of which were first described by Berkeley and Broome under Lepiota or under Agaricus. For the Neotropics, over 90 Lepiotas have been cited (see Appendix II). Essentially, these are species included in the works of Dennis and Pegler from the Caribbean and coastal Venezuela.

From Colombia the only reports are those of Pulido (1983) who included Lepiota subgranulosa Murr. from near Bogotá and Macrolepiota procera (Scop.:Fr.) Sing. from Facatátiva. Other reports include: Rugosospora pseudorubiginosa (Cifuentes and Guzmán) Guzmán and Bandala, cited by Guzmán et al. (1989), and by Velásquez et al. from near Medellín, and Lepiota quintanaroensis Guzmán-Dávalos and Guzmán, Lepiota serena (Fr.) Sacc., Lepiota montagnei (Kalchbr.) Sacc., and Lepiota subflavescens Murr., cited by Velásquez et al. (1989).

Although, most species of Lepiota have been reported as saprophytic, Trappe (1962) reported Macrolepiota procera and Lepiota subgracilis Kühn.: Wass. as ectomycorrhizal. The genus contains many edible species, but many others are very poisonous producing the same syndrome as Amanita phalloides (Vaill.:Fr.) Secr.: Schummel. In South America, L. locaniensis Espinosa, has been reported as poisonous (Singer, 1986). Furthermore, many species of

Lepiota produce extracellular enzymes responsible for lignin degradation which provide information on the role of the genus within the ecosystem. Some species of Leucoagaricus are cultivated and used as food by ants (Hervey *et al.* 1977).

Since the genus Lepiota has not been extensively and specifically studied in the Neotropics, this preliminary study, documenting the genera and the species found in Colombia, constitutes the base for further investigations of the group in the country and in the Neotropics in general. During this project extensive field work was carried out in a wide variety of habitats in Colombia, where approximately 125 collections were made and preserved. Several axenic tissue isolates were attempted, and spot tests for phenoloxidase activity were performed on fresh basidiomata of several collections, when sufficient material was available. In addition, in order to document geographic distribution of the species, collecting was carried out in Costa Rica, Ecuador and Bolivia.

To clarify the nomenclature and the taxonomy of the group, the extant types of Lepiota and related taxa were examined. The examination of the types, based on the modern taxonomy of the group, indicates that several new combinations should be made and that some hitherto accepted names are synonyms of taxa previously described.

Area of study

Colombia is located in the northwestern corner of South America within the following geographical coordinates: 12°30′40" N latitude; 4°13′30" S latitude; 66°50′54" W longitude; and 79°01′23" W longitude. It is the only South American country with a coastline on both the Atlantic and Pacific oceans. It is bounded by Panama to the northwest, by Venezuela to the east. Its southeast boundary with Brazil lies in the Amazon basin, and in the south it borders with Peru and Ecuador. Its total area is 1,138,914 km^2.

The tectonic history of Colombia presents one of the most complex geological systems in the northern Andes (van der Hammen, 1961). Beginning in the Upper Cretaceous, the first significant geosyncline separated portions of northern and southern Colombia. However, it was not until the mid Eocene that the first Andean formation appeared. By the Miocene, the Cauca and Magdalena valleys developed providing further partitioning. At the end of the Tertiary, at the Pliocene-Pleistocene boundary, major uplifts ocurred associated with the increased volcanic activity. The geology and paleoecology of the late Pleistocene has been well documented in Colombia in detailed studies by Van der Hammen and associates (see Van der Hammen and Cleef, 1986). The geological history of Colombia that includes the uplifts of the cordillera system (Occidental, Central and Oriental), and past lowering of vegetation belts leads to the formation, development and great diversification of plants and animals in a relatively short time (Gentry, 1982; Forero, 1988).

Colombia is divided into four topographic regions (Fig. 1): Pacific Coast (Chocó), the Atlantic Coast (Caribbean), the Andes and the eastern lowlands. Despite the variable climatic conditions for these regions, the rainy season and the dry season are well defined.

The Pacific coastal region of Colombia with an area of 70,806 km^2 (6% of the total surface of the country), is reduced to a narrow, irregular belt of lowlands between the Cordillera Occidental and the Pacific ocean from Panama to Ecuador. This region commomly called Chocó, constitutes the wettest part of the Neotropics (Gentry, 1982), with a rainfall of ±10,000 mm per year. It is well known because of its richness in vascular plants and pteridiophytes with a high level of endemism (Forero and Gentry, 1989). Near the Ecuadorian border this coastland extends inland from the Pacific sometimes as much as 100 km. This apparent flat platform is interrupted by spurs of the western Cordillera and by isolated peaks separated from one to another by a network of rivers and creeks. The Serranía del Darién does not exceed 400 m in altitude, although some peaks to the north are higher than 1,000 m.

The Atlantic region or Caribbean Coastal Plain, interrupted by the Sierra Nevada de Santa Marta, extends from the Sinú River to La Guajira Peninsula with an area of 101,118 km^2 (9% of the country surface). It is a level or moderately hilly region that comprises the flooded depression of Magdalena-Cauca-San Jorge rivers, the hilly region extending from the Departamento de Córdoba to the Departamento del Atlántico which includes the Serranias de Abibe, San Jerónimo, San Jacinto, Piojó and Santa Rosa, the Delta del Magdalena and the Guajira Peninsula. Generally this area is semi-arid and open and partly marshy along the rivers. Much of the Guajira Peninsula is arid; the Serrania de Macuira, in the north, constitutes an "island" covered by dense vegetation which is completely different from the surrounding deserts (Forero, 1989).

The Andean region with a surface of 372,150 km^2 (33% of the continental surface of the country) embraces the mountain system of the Andes which is divided into three different branches in Colombia (Cordillera Occidental, Cordillera Central, and Cordillera Oriental), the interandean valleys of Cauca and Magdalena rivers, and the isolated mountains of Sierra Nevada de Santa Marta and Sierra de La Macarena. These cordilleras, have an average of altitude of 3200-3500 m, with the high peaks, the interandean valley and the abrupt slopes, creating a great diversity of ecological conditions. The highest peaks, Pico Colón (5800 m) and Pico Bolívar (5575 m), are found in the Sierra Nevada de Santa Marta. The Sierra Nevada de Santa Marta appears like an island in the northern part of Colombia, without connection to any of the three cordilleras, and is considered to be part of the central cordillera. The eastern cordillera continues into Venezuela as Cordillera de Mérida.

The eastern lowlands range from 100-250 m above sea level, but may reach up to 1200 m in the Sierra de la Macarena (Departamento del Meta). It comprises the Llanos Orientales located in the Northeast with an area of 266,300 km^2 (23% of the country surface), and the Amazonas forest covering the Southeast with an area of 331,220 km^2 (29% of the total surface of the country). The Sierra de la Macarena and other isolated hills are considered to be the western extreme of the Guayana Highland.

The great variety of climatic conditions, habitats, and microhabitats provides a rich diversity of vegetation types with 24 major zones based on the Holdridge System (Espinal, 1977; 1990). According to Forero (1988) there has been an increase in the botanical exploration in the last three decades and the vascular plant flora for the country has been estimated at 35,000 species, yet little is known about of agaric mycota of the region.

The first major mycological exploration of the country published by Chardon and Toro (1930) reported 384 species of fungi of which 47 were new for science and 248 were new records for the country. Only four species of Agaricales belonging to one genus (Panus) were reported in this work. During the last several years an effort has been made to document the Colombian Agaricales. Concentrated field work has uncovered numerous collections of novel taxa. Many of these taxa have been described recently by specialists or they represent new records and extend the geographical distribution of several genera and species (Franco-Molano, 1993; Guzmán et al., 1989; Halling, 1989a, 1989b, 1992, 1993; Halling and Ovrebo, 1987; Horak and Halling, 1991; Pulido, 1983; Saldarriaga et al., 1988; Singer et al., 1990; Tulloss et al., 1992; Velásquez et al., 1989). So far a published mycoflora or annotated check list for the country does not exist. However, a pre-monographic work on *Amanita* was published by Tulloss *et al.* (1992).

Field trips were planned during the rainy season which varies according to the topographic region, March to May and September to November. Collections were made from 0 to 3000 m at 75 localities in to 11 departments in the four topographic regions (Fig. 1). The most intensive work was carried out in the Departamentos Antioquia and Valle. Because of the trememdous altitudinal gradients, different types of vegetation were visited: savanna, gallery forests, mixed hardwood forests, coniferous forests, *Quercus* and *Trigonobalanus* forests. Pulido and Boekhout (1989) and Boekhout and Pulido (1989) observed that the distribution of agarics along selected Andean transects depend on the altitude correlated with changes in the phanerogamic vegetation. Collecting of *Lepiota* s. l. was more successful in low altitudes, from sea level to 1000 m, with the diversity decreasing as the altidude increased.

Although, over 90 species of *Lepiota* s.l. have been described from the Neotropics, *Lepiota subgranulosa* Murr. and *Macrolepiota procera* (Scop.:Fr.) Sing. cited by Pulido (1983), *L. quintanaroensis* Guzmán-Dávalos and Gúzman, *L. serena* (Kalchbr.) Sacc., *L. subflavescens* Murr. cited by

Velásquez et al. (1991), and Rugosospora pseudorubiginosa (Cifuentes and Guzmán) Guzmán and Bandala cited by Guzmán et al. (1989) and by Velásquez et al. (1991) are the only taxa of Lepiota s.l. previously cited from Colombia.

Taxonomic and nomenclatural history of the group

The name Lepiota was first used by Persoon (1797) to include agarics characterized by having an annulate stipe and lacking a volva. Since the color of the spores was not considered, Agaricus campestris, a species with brown spores, was including in this group.

In Synopsis Methodica Fungorum (1801), Persoon used the name Lepiota as the first section of Agaricus, and based on spore color, transferred A. campestris to his section Pratella. Fries, in Systema Mycologicum (1821), gave a tribal designation to Lepiota in the series Leucosporus of the genus Agaricus, and S. F. Gray (1821) raised it to a generic level. Based exclusively on macromorphology, Gray's definition of the genus included species having a fleshy pileus; lamellae equal in length or mixed with lamellulae, juiceless, and not variegated; stipe central, annulate, and without volva; wholesome. Later, Fries (1874) based his six groups on pileus surface or annulus morphology or both. He included Agaricus molybdites but did not mention its green spore color. Later, Massee (1898) created the genus Chlorophyllum as analogous with the genus Lepiota, but by distinguished the former by the green gills and spore deposit.

Patouillard (1888), recognized the importance of some microscopic characters and erected the genus Leucocoprinus to place those species of Lepiota with a germ pore. Fayod (1889) created the genus Cystoderma based on microscopic studies as well, and placed emphasis on the structure of the universal veil. Cystoderma was disregarded by several authors because, according to Smith and Singer (1945), features mentioned by Fayod such as the differentiated cortex and pith of the stipe, fragility of lamellae, and the branching of hyphae forming the subhymenium, do not differentiate Cystoderma from other genera of gill fungi. The regular hymenophoral trama and the spore characters, as described by Fayod, are also found in Lepiota. However, Fayod's characters gained importance as microscopic studies were included in the taxonomy of fungi. Now the feature os a ramose subhymenium is one of the arguments used to place the genus Cystoderma in the family Tricholomataceae, rather than Agaricaceae (Bas et al., 1988), where it has been currently placed.

Earle (1909) erected the genus <u>Limacella</u> which, initially, differed from <u>Lepiota</u> in having a viscid to glutinous pileus surface. In 1913, Maire pointed out the presence of a divergent hymenophoral trama that made this genus more closely related to <u>Amanita</u> than to <u>Lepiota</u> in the restricted sense (Smith, 1945). In pioneering works on <u>Lepiota</u> (Berkeley and Broome, 1871; Saccardo, 1887-1905; Morgan, 1906, 1907, Murrill, 1912, 1914; Kauffman, 1918; 1924; Beeli, 1927, 1932, 1936; Lange, 1935), the species descriptions were compiled based on macroscopic features such as pileus and annulus morphologies; none or few microscopic features were included. Morgan (1906, 1907) arranged the species of <u>Lepiota</u> into three sections based on the mode of development of the partial veil and the manner of its rupture, but disregarded the genera <u>Cystoderma</u> and <u>Limacella</u>. Murrill (1914) utilized the traits of Friesan tribes for the limitations of species, placing viscid species in the genus <u>Limacella</u>. Kauffman (1918) divided the genus in three groups based on the characters of the cuticle of the pileus or of the veil. Kauffman (1924) supported Morgan's classification of the group based on the morphological development. His classification was based on the features of the universal and partial veils, including section <u>Viscidae</u> and section <u>Lubricae</u> ignoring, in this way, the genus <u>Limacella</u>. Lange (1935) recognized <u>Limacella</u> as a genus, with

Cystoderma and Leucobolbitius (Leucocoprinus?) as subgenera, and split the true lepiotas in three sections. Spore shape and size distinguished two of these sections, while the third section, Micaceae, was characterized by a cellular cuticle. One of the most important contributions to the taxonomy of the group was given by Kühner (1936). Although disregarding Cystoderma, he gave great importance to the cuticle of the pileus and to the consistency and morphology of the annulus in mature specimens. In addition, he included microscopic characters such as arrangement of lamellar trama; spores, basidia, and cystidia shapes and sizes, and reaction of the spores in Cresyl blue. Since then, the classification of Lepiota has been primarily based on his scheme with some modifications (Locquin, 1945; Kühner and Romagnesi, 1953).

Smith and Singer (1945) emended the genus Cystoderma to include species with a cellular cuticle and attached lamellae, excluding Lange's section Micaceae. Singer (1946) created the genus Macrolepiota for those species of Lepiota whose hyphae possess clamp connections, spore deposits are white to cream, and having giant spores with a metachromatic endosporium. Singer (1948) raised to generic level, Locquin's subgenus Leucoagaricus and characterized it by having a white, cream or pink spore deposit, germ pore, and metachromatic endosporium. Singer (1952) created the genus *Cystolepiota* characterizing its species by having habit and appearance as in *Lepiota* and epithelial epicutis of pileus, formed exclusively by sphaerocysts. Kühner and Romagnesi (1953) based their classification mainly on the reaction of the spore to Cresyl blue, the presence or absence of a germ pore and size of the spores, and the structure of the epicutis, recognizing six sections and seven subsections. Smith (1954) split the genus *Lepiota* into two subgenera, namely *Leucocoprinus* and "*Eu-Lepiota*" based on the thickness of the spore wall and the presence or absence of an apical germ pore. Cuticle and spore properties, or both, were used as sectional characters within the subgenus "*Eu-Lepiota*". Locquin (1956) divided the genus into seven subgenera delimited by the size of the spores, presence or absence of a germ pore, thickness of the spore wall, presence or absence of clamp connections, and type of pileus cuticle. Furthermore, the shape of the spores and, in some cases, the color of the lamellae delimited some of his sections. Singer and Grinling (1967) created the genus *Hiatulopsis* characterized by having globose to sub-globose spores with a heterogeneous, finely ornamented spore wall. Heinemann (1973b) created the genus *Rugosospora* based on the spore ornamentation of a *Leucocoprinus*-like fungus. Heinemann (1978) also erected the genus *Sericeomyces* corresponding to Kühner's sect.

Sericellae. This genus has been considered as a subgenus of *Leucoagaricus* by Candusso and Lanzoni (1990).

In addition, several other genera belong to the Lepiotaceous group. Singer (1944) created the genus *Smithiomyces* delimited by its heteromerous structure of the fragments of veil on the surface of pileus, inamyloid spores, and unpigmented basidiocarps. Singer (1959) created the genus *Volvolepiota*, which differs from *Macrolepiota* in having a well-defined volva. The genus *Chamaemyces* Batt.: Earle in Earle (1909) was characterized by the inamyloid spores, hymeniform pileal epicutis and adnate lamellae. Although this genus has been placed in Singer's tribe *Lepioteae*, it probably belongs to the tribe *Cystodermateae* due to the adnate lamellae as originally described.

Following Kühner (1936) and Kühner and Romagnesi (1953) the modern classification of the group is based on the structure of the pileus surface, spore size, spore shape, spore wall reactivity in Melzer's reagent and cresyl blue reagents, presence or absence of a germ pore, and presence or absence of cystidia.

The genus *Lepiota* s.l. has been placed in the family *Lepiotaceae* which was apparently first used by Roze in

1876 (Singer, 1949). Although this family seems to be still waiting for validation, it has been used by Kühner and Romagnesi (1953), Sundberg (1967, 1971) and by Smith and Sundberg (1979). Kühner and Romanegsi (1953), disregarding the color of the spores, included the genera *Agaricus*, *Cystoderma* and *Lepiota* in the family *Lepiotaceae*. Singer (1949, 1962, 1975, 1986) used the family *Agaricaceae*, and divided it into four tribes: *Leucocoprineae* Sing., *Lepioteae* Fayod, *Agariceae* Pat., and *Cystodermateae* Sing. Although usually modified, Singer's classification of the group has been widely used (Bon, 1981; Guzmán and Guzmán-D., 1992; Heinemann, 1973a, 1973b, 1977, 1978, 1980, 1989; Kühner, 1980; Pegler, 1977, 1983, 1986). In the first world monograph of *Lepiota* s.l. (Candusso and Lanzoni, 1990) the genera *Lepiota* s.s., *Melanophyllum*, *Cystolepiota*, *Chamaemyces*, *Leucoagaricus*, *Leucocoprinus* and *Macrolepiota* were included. Those workers accepted the family *Agaricaceae*, as suggested by Singer (1986).

Typification of the genus

Since no type species was designated by Gray (1821), Singer and Smith (1946) selected *Lepiota colubrina* (= *Lepiota clypeolaria*) as lectotype from among the species included by Gray and not considered belonging in other genera.

Donk (1962) rejected Lepiota colubrina as a lectotype, pointing out that since Gray obtained the epithet directly from Persoon rather than from Systema Mycologicum, the lectotype should be selected from the species mentioned by Persoon (Agaricus procerus Scop., Agaricus conspurcatus Willd., Agaricus cristatus Bolt.). Donk (l.c.) accepted A. procerus as lectotype because it was the first type, chosen by Earle (1909) from the species mentioned by Persoon.

Classification of Lepiota s.l.

Since the creation of the genus, several classifications have been published [e.g. Morgan (1906, 1907), Murrill (1914), Lange (1935), Bon (1981), Candusso and Lanzoni (1990), and Guzmán and Guzmán-Dávalos (1992)]. However, Kühner (1936), Locquin (1945) and Singer (1949, 1962, 1975, 1986) have been the basis for several works.

Kühner (1936):

Genus Lepiota
  - Sect. Granulosae Fries
  - Sect. Micaceae Lange

Sect. Echinatae Fayod
Sect. Sericellae Kühner
Sect. Lepiotellae Gilbert
Sect. Integrellae Kühner
Sect. Cristatae Kühner
Sect. Ovisporae Lange
Sect. Clypeolariae Fries
Sect. Stenosporae Lange
Sect. Pilosellae Kühner
Sect. Annulosae Fries
Sect. Procerae Fries
Sect. Striatae Murrill

Genus Limacella Earle

Locquin (1945):
Genus Lepiota
Subgenus Eulepiota Fries
Subgenus Micacystis Locquin
Subgenus Lepiotula (Maire) Locquin
Subgenus Lepiotella Gilbert
Subgenus Integrella Kühner
Subgenus Pilosella Kühner
Subgenus Sericella Kühner

Genus Leucocoprinus Pat.

Subgenus Euleucocoprinus

Subgenus Leucoagaricus Locquin

Subgenus Hiatula Fries

Subgenus Leucobolbitius Lange

Genus Cystoderma Fayod

Singer (1986):

Tribe Leucocoprineae Singer

Genus Clarkeinda O. Kuntze

Genus Chlorophyllum Massee

Genus Volvolepiota Singer

Genus Macrolepiota Singer

Genus Leucoagaricus (Locquin) Singer

Genus Sericeomyces Heinemann

Genus Leucocoprinus Patouillard

In this work, the genus Rugosospora (Heinemann, 1973a) has been added to this tribe. Furthermore, the genus Chloroplepiota Sathe & Desphande also belongs to this tribe (Guzmán and Guzmán Dávalos, 1992).

Tribe Lepioteae

Genus Cystolepiota Singer

Genus Lepiota (Pers.) S. F. Gray

Genus Chamaemyces Batt.: Earle

Genus Smithiomyces Singer
Genus Hiatulopsis Singer and Grinling
Genus Januaria Singer

Tribe Cystodermateae (See below)
Genus Cystoderma Fayod
Genus Phaeolepiota Maire
Genus Dissoderma (Smith and Singer) Singer
Genus Squamanita Imbach
Genus Ripartitella Singer
Genus Horakia Oberwinkler
Genus Pseudobaeospora Singer

I agree with Bas (1988, 1990)), that except for the genus Squamanita which is placed in the family Squamanitaceae, the genera Cystoderma, Phaeolepiota, Dissoderma, Ripartitella, Horakia, and Pseudobaeospora are best placed in the Tricholomataceae.

Ecological considerations

The species of Lepiota s.l. are distributed worldwide but they predominantly occur in the tropics and subtropics (Patouillard, 1888; Pegler, 1972, 1983; Horak, 1980a; Guzmán and Guzmán-Dávalos, 1992; Guzmán-Dávalos and Guzmán, 1979, 1982; Singer, 1986) and in greenhouses in temperate areas. Although the species of Lepiota s.l. do not fruit with regularity, in tropical areas different species can be found in humid places throughout the year. They are predominant in lowlands and diversity decreases with altitude. Species of Leucocoprinus are more abundant between 0 and 1000 m, while species of Macrolepiota seem to be more common above 2500 m. Species of Leucoagaricus are more frequently found between 1000 and 2000 m and the species of Lepiota s.s. are more abundant from 0 to 1200-1500 m.

According to Bon (1981), most tropical species of Lepiota s.l. are humicolous and thermophilous, playing an important role in nutrient retention and recycling in tropical, subtropical and temperate regions (Guzmán and Guzmán-Dávalos, 1992). Although most species of Lepiota have been reported as saprophytic, Trappe (1962) reported Macrolepiota procera and Lepiota subgracilis Kühn.: Wass. as an ectomycorrhizal agaric.

With regard to substrate preferences, the species of Lepiota s.l. seem not to be very specific. In my work I found the same species [(e. g. Leucoagaricus rubrotinctus (Peck) Singer)] on soil of Pinus forest, mixed hardwood forest, and outside of Quercus forest. Furthermore, Lepiota rubiginosoides sp. nov., was found on palm leaves, and on soil in mixed forest. Most species of *Leucocoprinus* grow in soil rich in humus; they also grow in soil in potted plants and backyards in the tropics. *Chlorophyllum molybdites* (Meyer:Fr.) Massee and *Leucoagaricus hortensis* (Murril) Pegler grow on grass. Most species of *Macrolepiota* grow in *Pinus* forests.

The genus contains many edible species, but many others are very poisonous producing the same syndrome as *Amanita phalloides* (Vaill.:Fr.) Secr.: Schummel. In South America, *L. locaniensis* Espinosa, has been reported as poisonous (Singer, 1986). Furthermore, many species of *Lepiota* produce extracellular enzymes responsible for lignin degradation which provide information on the role of the genus within the ecosystem.

Lepiota **s.l. and ants relationship**

The cultivation of fungi by some species of ants has been frequently studied (Martin, 1970; Weber, 1957, 1966; Stevens, 1983). The leaf-cutting ants of the genera *Atta*, *Acromyrmex*, and *Cyphomyrmes*, cultivate fungi on leaf and flower parts in an underground garden where the fungus mycelium forms hyphae with inflated tips [gongylidia (Stevens, 1983), bromatia or staphylidae (Hervey *et al.*, 1977)] used by the ants as a major source of food.

The fungus-growing ants are predominantly Neotropical in distribution, but they also occur exclusively in the Western Hemisphere (Martin, 1970). Basidiomata of the fungus were observed for the first time in a nest of *Acromyrmes disciger* by Möller in Santa Catarina, Brasil (Ramos, 1981) who identified it as *Rozites gongylophorus* Möller. Saccardo (1895) transferred it to *Pholiota* (Fr.) Kummer. Although the fungus was described as having brown spores (Saccardo, 1895), Heim (1957) placed it in *Leucocoprinus*, and Singer (1975) considered it as *Leucoagaricus*. I have not seen representative material.

Kreisel in 1972 (Romero *et al.*, 1987) described two Deuteromycetes: *Attamyces bromatificus* and *Phialocladus zsoltii* that were cultivated by *Atta insularia*. Singer (1986) considered *Attamyces bromatificus* to be the imperfect stage of *Leucoagaricus*. Hervey *et al.* (1977) reported *Attamyces bromatificus* and *Lepiota* sp. from other ant's nest. Moreover, *Leucoagaricus weberi* Muchovej, Della Lucia and R. Muchovej was described from a nest of *Atta sexdens* subsp. *rubripilosa* (Muchojev *et al.*, 1991).

During this work I did not have the opportunity to study basidiomata of *Lepiota* s.l. associated with ants. In Carimagua, Colombia, I saw mycelium growing in about ten nests of Acromyrmes sp., however all attempts at cultivation of fungus have failed (O. Guzmán, pers. information) and the fungus remains unknown. In the Sierra Nevada de Santa Marta, I collected several young and mature basidiomata of Agaricus sp., associated with ant nests, but the ants were lost before identification.

CHAPTER II

Material and methods

This study has been done based on fresh specimens collected by the author and collaborators in a wide variety of habitats in Colombia. Freshly gathered basidiocarps were wrapped in wax paper and carefully taken to base stations.

Once in the base station (hotel room, laboratory or a small space in a tent) all fleshy collections were studied by using the following procedure: 1) Photographs of each collection showing important macroscopic characters were taken with a Nikon FM2 35 mm camera plus flash attachment, through a 55 mm Nikkor Micro lens, using Kodachrome 64 color slide film. 2) Macroscopic characteristics were recorded for each collection with special attention given to size, shape, coloration and surface features of pileus and stipe; thickness, color and color change, and often odor and taste of context of pileus and stipe; attachment, spacing, shape, color and color changes, and margin of lamellae by using the terminology of Snell and Dick (1971) and Largent _et al._ (1977). Furthermore, a color standard (Kornerup and Wanscher, 1983) was used for accurate color descriptions. 3) Spore-prints were attempted on white bond paper or in sterile Petri plates for all collections with more than one basidiocarp in order to obtain spore color and to prepare samples for single spore cultures. 4) If sufficient material was available, a portion of the basidiocarps were tested with KOH and NH_4OH. 5) Tissue cultures of <u>Lepiota</u> and related genera were performed by placing small portions of clean lamellae or sterile tissue in malt agar (Nobles, 1948, 1965) supplemented with o-hydroxydiphenyl (o-phenylphenol) (1 mg/L, prepared by dissolving 1 gm of o-phenylphenol in 100 ml of 50% ethanol) and streptomycin (50 mg/L), added as biocides to keep unwanted fungal and bacterial contamination to a minimum during initial isolation. Malt agar suplemented with benomyl (1 mg/L) (Maloy, 1971) was also used. 6) The collections were labeled, dried with warm air, and sealed in plastic bags, for protection and transport to the laboratory at The New York Botanical Garden.

Description of micromorphological features were based on examination of small pieces of the dried material which were immersed in 95% ethyl alcohol for few seconds to facilitate reviving. The pieces of material were then placing in water for at least one minute before sectioning. Hand sections, following the instructions of Largent <u>et al</u>. (1977), were made with double edge razor blades by slicing the material held in styrofoam or pith.

Sections to study the micromorphology were first mounted in distilled water to determine disposition, color, and characteristics of pigments. Then the sections were studied in either 3% KOH or 5% NH_4OH to observe changes in pigmentation, if any. These mounts were then infiltrated with ammoniacal Congo red in order to obtain more contrast for the micromorphology analyses. Sections were also mounted in Melzer's reagent to test for reactions to iodine, and in Cresyl blue to observe metachromasy.

The following sections were examined: 1) Tangential sections of pilei from which information on the structure of and cell types of pileipellis, characteristics of pileus trama, hyphal arrangement of hymenophoral trama and subhymenium. Furthermore, these sections were used in determining the ocurrence and morphology of basidia, basidioles, pleurocystidia, pileocystidia and pileocystidioid elements, pigment localization, and clamp connections. 2.) Scalp (paradermal) sections of pilei were made to obtain information about type and organization of hyphae near the margin. 3) Edge sections of lamellae provided information about presence or absence, sizes, shape and distribution of cheilocystidia and, if present, of the basidia. 4) Longitudinal sections of the stipitipellis were made to observe the arrangement and morphology of the hyphae as well as the presence or absence of clamp connections and of veil remnants. After the information from these sections was obtained, they were gently squashed and descriptions were written and illustrations were made using a drawing tube.

Basidiospores were examined from a spore print, if available, or from spores deposited on the pileus or stipe, or from a fragment of a lamellae. They were mounted in Melzer's reagent and the reactivity to iodine was recordered as amyloid, inamyloid, or dextrinoid. Information on shape, size, presence or absence of a germ pore, and spore wall features were also taken from these mounts. Twenty to 30 spores were measured and the mean value of length/width is given as ($\bar{Q}$). Metachromasy of the spores were recorded by placing a small fragment of lamellae in an aquous solution of NH_4OH for 5 min., transferred to 10% acetic acid for 5 min., and then placed in a drop of 1% Cresyl blue (Ruini, 1989). Also, cotton blue in lactic acid (Singer, 1986) was used to test the cyanophilous reaction of the spore wall.

Phenoloxidases analysis in basidiomata: Macrochemical tests were conducted, whenever possible, for laccase and tyrosinase production following the procedure developed by Marr et al. (1986). Reagents used were syringaldazine, p-cresol, prepared according to Marr (1979); reactions were recorded for 5, 15, 30, 60 and 90 minute intervals.

Scanning Electron Microscopic studies of the spore wall were done when ornamentation was suspected when viewed at 1000X under the compound microscope. The material for SEM studies were prepared as follow: lamellar fragments were 1) rehydrated for 20 min to 2 hours in 10% Na_4OH; 2) washed three times in distilled water, 5 min each; 3) fixed in 1% OsO_4 in 0.1 M sodium-phosphate buffer, pH 7.2; 4) rinsed with sodium phosphate buffer; 5) dehydrated in an ethanol series (10%, 30%, 50%, 70%, 90%, and three changes in 100%, 10 min at each time; 6) critical point dried. The lamellar fragments were mounted on aluminum stubs with double sticky tape, coated with gold and observed in a Jeol 3300 (New York Botanical Garden) or Amray 1830 (Lehman College) SEM at 15 kV.

In the presentation of results I included a distribution map only for <u>Rugosospora</u>, because it is the only genus from which I have seen the extant material.

CHAPTER III

Taxonomic features

The white to whitish spore deposit, free lamellae, central stipe, presence of an annulus and lack of a volva are the diagnostic features of Lepiota s.l. in the Friesian classification. However, as more macro- and micromorphological features have taken on taxonomic importance, the genus has been split into several segregate genera.

It is important to point out that no single morphological character differentiates genera within Lepiota s.l. It is the combination of characters or the interpretation of specific character states that will give us accurate generic diagnoses. The infrageneric variation of the characters and combinations of states will define species.

Macroscopic features

Basidioma Development

Although it has been stressed that ontogeny could clarify intergeneric and infrageneric taxonomic problems in Lepiota (Atkinson 1914, 1916; Kauffman, 1924) and in basidiomycetes in general (Singer, 1986), very few data have been published on development of basidiomata in Lepiota s.l. Atkinson (1914) studied ontogenetic development of three different forms of Lepiota clypeolaria (Bull.: Fr.) Kummer, placing more attention to the development of the veils. Later, Atkinson (1916) studied the ontogenetic development of Lepiota cristata (Alb. & Schw.: Fr.) Kummer, and Lepiota seminuda [Cystolepiota seminuda (Lasch.) Bon.] giving special attention to the development of the annulus and stipe covering in L. cristata and the formation of the universal veil in L. seminuda.

Reijnders (1963) reported that Lepiota sistrata (Lasch.) Gill. [Cystolepiota seminuda (Lasch.) Bon], L. hetieri Boud. [Cystolepiota hetieri (Boud.) Sing.], L. echinata (Roth.:Fr.) Quél., L. acutesquamosa (Weinm.) Gill., L. cristata (Alb. & Schw.:Fr.) Kummer, L. clypeolaria (Bull.:Fr.) Kummer, Leucocoprinus cepaestipes (Sow.: Fr.) Pat., and Macrolepiota rachodes were **bivelangiocarpous**. Singer (1986) reported Clarkeinda, Chlorophyllum, Volvolepiota, Leucocoprinus (except L. cepaestipes and probably Smithiomyces) to be **hemiangiocarpous**; Macrolepiota, Leucoagaricus, Cystolepiota, L. cepaestipes and Lepiota as mostly **bivelangiocarpous** while considering other types within these genera; Sericeomyces as **velangiocarpous**, and Chamaemyces as **monovelangiocarpous**. The development of Hiatulopsis and Januaria is unknown. Ontogenetic studies of basidioma are lacking that might add more information to the taxonomy and phylogeny the Lepiota s. l. However, since several genera share the same type of development, this character by itself will not define genera.

Basidioma stature and size

The species of Lepiota s.l. show considerable variation in stature and size of the basidiomata. Although, these features have limited taxonomic value, the species of Macrolepiota are characterized for having the biggest size within the group. Macrolepiota procera has been reported as possessing a pileus up to 40 cm diam and a stipe 10-40 cm long with a 1-4 cm width (Candusso and Lanzoni, 1990). Big basidiomata are also common in Chlorophyllum and Leucoagaricus; medium size to small basidiomata are common in the other genera of the group. Largent (1986) suggests several terms to describe the basidioma as a whole by correlating a series of features: presence or absence of an annulus or volva, consistency and attachment of the stipe, attachment of lamellae, shape of pileus, and type of pileal margin. In Lepiota s.l. the term lepiotoid is used to describe basidiomata possessing an annulus, lacking a volva, and having a centrally attached stipe and free lamellae; and the term pluteoid is used to describe those species also having a centrally attached stipe and free lamellae but lacking a well-formed annulus or with an evanescent annulus.

Pileus Features

Size and Shape. In Lepiota s.l., the size of the pileus is very variable. In the Colombian taxa, the pileus size ranges from 2 mm in Lepiota bettinae Dörfelt to ±20(30) cm in Chlorophyllum molybdites (Meyer: Fr.) Mass. The pileus shape varies from hemispheric, narrowly parabolic or convex to broadly conical in young specimens becoming plano-convex, plane or subumbonate with age. The margin of the pileus is inrolled, incurved to decurved in young basidiomata and becomes decurved to uplifted as the pileus expands with age. The edge of the margin may be entire, crisped, undulating, splitting radially at maturity, and often, especially in young specimens, appendiculate. The surface of the margin may be fleshy and smooth to finely striate or membranous to submembranous and long striate, sulcate or plicate. The membranous and plicate or long striate margin surface of Leucocoprinus has been used to distinguish it from Leucoagaricus (Smith and Shaffer, 1964; Singer, 1949, 1962, 1975, 1986; Heinemann, 1973b). Although the surface of the margin can help to place a fresh specimen within a genus, it is the combination of that surface with microscopic characters that insure an accurate determination. Macroscopically, Leucocoprinus, Hiatulopsis, and Januaria cannot be distinguished from one another, their determination is possible only after microscopic studies.

Surface. The surface of the pileus was used by Fries (1874) to separate the group into two large divisions: species with a dry pileus surface and species with a viscid pileus surface. The species with a viscid pileus surface belong to Limacella. The pileus surface of Lepiota s. l. is dull and dry in most species; a slightly viscid pileus surface is found in some species of Leucoagaricus section Rubrotincti (Bon, 1981). Although, the name Lepiota comes from the greek word "lepis" meaning scaly, the general appearance of the pileus surface depends on how the universal veil intergrows with the epicutis and how it breaks as the pileus expands. In Macrolepiota, Chlorophyllum and some Lepiota spp. (e.g. L. cristata), the epicutis of the pileus breaks from the margin toward the center into small to medium size scales, areolae or patches, leaving an entire center or "calotte." An epicutis with a pruinose to granulose aspect is found in some species of Cystolepiota and Leucocoprinus. A fibrillose epicutis that usually splits radially showing the subcutis or the context of the pileus is common in

Leucoagaricus. An appressed fibrillose-scaly to squarrose surface is found in *Lepiota* and *Rugosospora*, and a squamulose surface is found in *Lepiota*, *Leucocoprinus*, and *Leucoagaricus*. A glabrous, matted fibrillose surface can also be found in *Lepiota narinyensis* sp. nov. In one species, *Lepiota hemisclera* Berk. & Curt., the universal veil remnants on the pileus form conical to verrucose, detersile granules.

Color. The pileus color is very variable within the group. It ranges from shades of dark brown, yellowish brown or red brown especially in *Macrolepiota* and *Chlorophyllum* to white, whitish or different shades of red, purple, olive, orange or yellow. Although, color can be constant within a species, it may be affected by the age, handling, or other environmental conditions. Often, the color of the pileus is darker or brighter in young basidiomata and become paler with age. Mature pilei are more deeply pigmented at the center than they are toward the margin. *Leucocoprinus birnbaumii* (Corda) Sing., is very bright yellow when young and becomes yellow to pale yellow with age. *Leucocoprinus sulphurellus* Pegler, a pale yellow species, becomes blue green when handled. In *Leucoagaricus rubrotinctus* (Peck) Sing., the coral red color of the young pileus remains at the center and becomes paler toward the margin when mature.

Pileus context. The thickness of the pileus context has some taxonomic importance in the separation of the species of Leucoagaricus and Leucocoprinus. It can be very thick in Macrolepiota, Chlorophyllum, and some Leucoagaricus or very thin as it is in Leucocoprinus fragilissimus (Berk. & Rav.) Pat.

According to Singer (1986), color changes of the context of the pileus occur in several genera of the tribe Leucocoprineae. It has been used to recognize some species of Leucoagaricus (e. g. the L. badhamii complex, Reid, 1990). In addition, some Leucocoprinus spp. (e. g. L. sulphurellus) change color on bruising. Color changes have been reported for some other species of Lepiota s.s. (e. g. L. viriditincta (Berk. & Br.) Sacc. None of the Colombian taxa of Lepiota s.s. showed color changes of the pileus context.

The odor of the context in Lepiota is of little taxonomic value. Usually it is indistictive or fungal but fruity or fruity-alcoholic odors have been reported in Lepiota cristata. The taste has no taxonomic value. Probably because some species of Lepiota are poisonous, the taste is generally not recorded.

Lamellar Features

Attachment. Lamellae are truly free, never adnexed, adnate or sinuate. They can be very close to the stipe in most species of Lepiota, Cystolepiota, Leucoagaricus, Leucocoprinus, and Rugosospora, or remote and separate from the stipe by a "collarium" in Macrolepiota and Chlorophyllum.

Spacing. The lamellar spacing in mature pilei ranges from crowded to close. There are no taxa with distant or remote lamellae.

Edge. The lamellar edge ranges from smooth and even when no or small cheilocystidia are present to finely serrate or fimbriate due to the presence, in many cases, of very abundant and/or very long cheilocystidia. If lamellar edges are colored differently from lamellar faces, the lamellae are said to be marginate. Marginate lamellae may be taxonomically significant but only if constant through all basidiomata. This feature can be very variable becoming visible only near the edge of the pileus or in old basidiomata. Sometimes it can appear when the edge of the lamellae stain when bruised (e.g. the Leucoagaricus badhamii complex).

Color. The lamellar color is mostly white to cream or sometimes pinkish (e.g. Lepiota roseolamellata Dennis) or yellow to yellowish (e.g. *Lepiota flavidocana* Pegler, *Lepiota subflavescens* Murrill, *Leucocoprinus sulphurellus* Pegler) or pinkish buff and later pale to dark green (e.g. *Chlorophyllum molybdites*). The color of the lamellae may change on bruising or drying. The lamellae of *Chlorophyllum* stain reddish when bruised, and in some species of the *Leucoagaricus badhami* complex, the lamellae become red to orange and then black when bruised. In *Leucocoprinus sulphurellus* they turn green. In addition, the lamellae of *Leucocoprinus zamurensis* Pat. becomes pink on drying. The color and the color change of lamellae are taxonomically important at the species level.

Stipe Features

Size and Shape. The length and diameter of the stipe are of little taxonomic importance and are correlated with the size of the pileus. The stipe of the tallest Colombian taxa, *Macrolepiota colombiana* sp. nov., reachs up to 30 cm long and 3 cm diam at the apex while the stipe of the smallest one, *Lepiota bettinae* reaches a maximun of 1.5 cm long and 1 mm diam. The shape of the stipe varies from equal to abruptly bulbous. This character is more or less constant, but variations observed within a species limit its taxonomic importance.

Surface. Although, features related to the stipe surface are useful in species diagnoses, and should be considered useful in separating genera into sections, they have not been given the attention reserved for features of the pileus and are missing in most descriptions.

The stipe surface ranges from dull to shiny and from glabrous to pruinose, matted fibrillose, fibrillose, appressed fibrillose-scaly, squarrose, shaggy or ±areolate. Depending on the presence of a universal veil and on the manner of the separation of the pileus margin from the stipe, the stipe surface and the pileus surface may or may not share the same kind of tissue.

Color. This feature of the stipe surface depends on the development of the basidiomata. If the pileus surface and the stipe surface share the same kind of tissue, then the stipe, at least below the annulus, and the pileus are concolorous. When the stipe surface is developmentally different from the pileus surface, the color of the stipe may have the same color of the pileus but is usually paler, or it may range from white, whitish, yellowish or different shades of brown. Generally, the color of the stipe is paler at the apex and darker toward the base.

Veils

Singer (1986) pointed out that veils are important as protective layers in the primordia and juvenile stages of agarics. In mature basidiomata, the remnants of the veils that are more or less constant in location and structure are used in taxonomy. So far, two kinds of veils have been described: the partial veil and the universal veil.

Partial veil. Although Singer (1986) suggested use of this term in a limited sense, and only with respect to mature basidiomata, it has played an important role in the taxonomy of Lepiota s. l. The development of the partial veil or "annulus", and its appearance in mature basidiomata has been used in the classification of the group.

Fries (1836-1838) characterized four of the sections of Lepiota s.l. based on the fixed or moveable annulus, and its combination with the distribution of the universal veil on the pileus and/or the stipe. Section Proceri was characterized by a moveable annulus and a pileus surface different from the stipe surface. Section Clypeolarii was characterized with a fixed annulus and a universal veil confluent with pileus and stipe surfaces. Section Annulosi possessed a ±persistent annulus but the universal veil was not confluent with the stipe surface. Section Granulosi was distinguished by an annulus left on the stipe as a result of the rupture of the universal veil with the expansion of the pileus.

According to Morgan (1906, 1907), the development of the partial veil and the different ways of its rupture are the basis of three sections in his classification. In the first section, Annuli inferi, the universal veil that covers the pileus and the stipe forms the outer layer of the annulus (e.g. Lepiota clypeolaria). In the second section, Annuli mobile, the universal veil is covering the pileus. The annulus is described as a continuation of the outermost layer of the stipe connected to the pileus only by its upper border (e.g. Leucoagaricus rubrotinctus). In the third section, Annuli superi, the annulus is formed at the apex of the stipe, from a tissue underneath the stipe surface which is connected at first to the edges of the lamellae and then forms a membrane that covers the hymenium. With the expansion of the pileus, this membrane breaks at its connection with the edge of the lamellae and remains attached to the upper end of the stipe hanging down from it (Lepiota avellanea Clements).

Kühner (1936, 1980) defined the partial veil as the white membrane formed as the continuation of the edge of pileus with the surface of the stipe and covering the pileal cavity where the lamellae develop. This partial veil, in some species, is covered by the continuation of the universal veil from the pileus into the stipe. In some species, it is formed by thin and incoherent tissue which with the expansion of the cap and elongation of the stipe forms a fibrillose annulus often visible only under a lens. In other species (e.g. Lepiota clypeolaria), it is formed by floccose or densely fibrillose tissue that breaks into tufts with the elongation of the stipe forming a woolly annulus. The superior border of each tuft shows remnants of a tissue analogous to the tissue covering the pileus (universal veil). In some species (e.g. Lepiota cristata) the partial veil is formed by a coherent tissue which forms a membranous annulus on the stipe. This partial veil breaks circumferentially at two points, at its juncture with the pileus and at the juncture of the stipe, and remains attached to the stipe by a few internal fibrils giving an evanescent annulus. A permanent annulus results from the increased thickness of the internal fibrils that affix it to the stipe. In a more complicated annulus (e.g. Macrolepiota procera), the portion nearest the stipe is very thin and the external edge is thick and fleshy. It separates circumferentially from the stipe and remains on it as a moveable annulus. The outside tissue of this annulus corresponds to the marginal part of the pileus surface. Although Kühner used the aspect of the annulus in mature basidiomata in the classification of the group, he considered that the final appearance of the annulus depends on the characteristics of each individual, the cohesion of the tissue forming the epicutis, the elongation of the stipe, and probably the environmental conditions.

Because the development of only a few species of Lepiota have been studied from the primordium (Atkinson, 1914, 1916), there is not sufficient information about ontogenetic development of the partial veil. However, Kühner's (1936) appreciation of the formation of the annulus and its appearance in mature basidiomata is rather complete and somehow includes Fries' and Morgan's classifications. Although, the annulus of the Colombian species of Lepiota s.l., included in this work fit into many of Kühner categories, I have not used this feature taxonomically because within the taxonomic levels used in this work, it is possible to find more than one of the Kühner's categories. In addition, information on the structure of the annulus is lacking in most type descriptions.

Excluding Morgan's section Annuli superi which probably described the annulus of some species of Amanita and Agaricus, Fries, Morgan and Kühner have given some bases for further studies on the partial veil which could add very valuable information to the group at generic, sectional and specific levels. In many species of Lepiota, the veils are delicate and can be lost due to rain, insects, grazing by invertebrates, poor handling, or other factors. Because of poor observation in the past, the macromorphological appearance of the annulus is missing in most descriptions. During the course of this study, I found that the annulus is very variable within a genus and it is rather constant at the specific level. It is necessary however to gather more information before velar development is completely understood.

Universal veil

The universal veil is defined as the outermost membrane surrounding the primordium of many agarics that protects the developing basidioma and reduces the exposure time of the hymenium to the environmemt (Watling, 1985).

Fries (1821) separated Amanita from Lepiota based on the universal veil. In Amanita the universal veil is discrete from the pileus surface and forms a volva while in Lepiota it is contiguous to and concrescent with the pileus surface; standing on a ruptured, early fugacious annulus. Atkinson (1914) pointed out that the universal veil seen in young specimens grows together and becomes concrescent with the pileus and stipe surfaces in L.

clypeolaria, whereas, in Amanita there is a gelatinization of an inner layer of the universal veil which causes it to rupture to form the volva. In other studies, Atkinson (1916) observed that the universal veil in L. cristata is poorly developed and not noticeable on the stipe and annulus while it becomes concrescent with the surface of pileus, and that in L. seminuda the cells of the universal veil become very large and globose to subglobose forming a powdery or mealy layer covering the pileus and stipe.

Although, there is a general recognition that a universal veil exists in Lepiota s.l., its ultimate disposition is variable and Fries' characterization of the universal veil being concrescent with the pileus surface does not fit in all species.

Fries (1836-1838) characterized his section Proceri which includes species of Macrolepiota as wrapped by a complete volva when young and the remnants of this volva on pileus which he called a "calyptra" as being adnate in mature basidiomata. Similarly, in M. colombiana first described in this work, I observed fragments of a white, membranous universal veil on the pileus and stipe surfaces. Kühner (1936) observed that M. rachodes was initially wrapped by a thin, white universal veil which disappeared in mature basidiomata. He also reported some fragments of a universal veil on the pileus of *M. excoriata*. It is probable that Fries was confused with his general appreciation of the universal veil of *Lepiota* and the appreciation of the universal veil in his section *Proceri* because in 1874 he indicated (contrary to his definition in 1836-1838) that in this section the "calyptra" was connate with the pileus surface. Some other cases also show a universal veil not concrescent with the pileus surface. Menier (1889) pointed out the presence of the universal veil in young basidiomata of *Lepiota littoralis* and that only a few remnants remain at the base of the stipe at maturity. I have observed in *L. hemisclera* that the universal veil remains as detersile scales on the pileus, base of the stipe and lower edge of the annulus. Furthermore, similar to what happens in *Amanita*, in *Volvolepiota* spp. and in *Lepiota volvatula*, the universal veil forms a volva.

During this work, it was not possible to study the development of any species from primordium to adult because most of the culture attempts failed or primordia did not form, or because the collections consisted only of mature basidiomata. Based on the collections examined which included Colombian collections, types, and collections from other areas, I observed that the ultimate disposition of the universal veil is variable. In *Macrolepiota colom-*

biana and in *Lepiota hemisclera* as noted above, the universal veil is not concrescent with the pileus. However, in these cases, the pileus and the stipe surfaces share the same kind of tissue.

Assuming that Atkinson's observations (1914, 1916) on *Lepiota clypeolaria* were correct, then species of section *Lepiota* and section *Stenosporae* of *Lepiota* s.s., and the species belonging to *Cystolepiota*, have a universal veil concrescent with the pileus and stipe surface. However, there are not enough ontogenetic studies to show that it is the universal veil and not the epicutis itself which gives the final appearance to the mature basidiomata.

Microscopic features

In *Lepiota* s. l., as in most Agaricales, the circumscription of species and genera is more accurate based on microscopic characters. Since complete studies of the microscopic characters for delimitation of genera and species are missing for most types, it has been difficult to name Colombian collections. Type studies including microscopic characters indicate that several new combinations should be made and that some taxa with hitherto accepted names are synonyms of taxa previously described.

Basidiospores

Spore print color. Except for Clarkeinda, Chlorophyllum, and Chlorolepiota, which are characterized by their green spore print, most of the species of Lepiota s.l. produce a white spore deposit. However, spore color may range from white, buff, pale yellow, pale pink, cream, cream-orange to lilac. The spore print color has value at the generic level and is included here as indicative of that taxonomic level. It is the first characteristic emphasized for separation of the genera belonging to the tribe Leucocoprineae.

Spore shape and size. The spore size and shape are important in the taxonomy of Lepiota s.l. Lange (1935), arranged the Friesian classification of the group into three sections (Procerae, Clypeolariae, and Micaceae) based on the size and shape of the basidiospores.

In Lepiota s. l. the spore shape, ranges from globose to subglobose in Hiatulopsis; ovoid, broadly ellipsoid to subcylindric in Macrolepiota, Chlorophyllum and Leucocoprinus; broadly ellipsoid to ellipsoid in Leucoagaricus, Rugosospora, and Cystolepiota. In Lepiota s.s. (Bon, 1981; Singer, 1986), species of section Lilaceae, Amyloidae, Ovisporae, Anomalae, and Amylosporae, and some species belonging to section *Echinateae*, are characterized by having ovoid, broadly ellipsoid to ellipsoid basidiospores. Section *Lepiota*, and most of the species of section *Echinatae*, have fusoid basidiospores and section *Stenosporae* and section *Cristatae* are characterized by spurred or stenosporic basidiospores.

Spore wall. Features of the spore wall and reactions to microchemical tests are essential in the taxonomy of *Lepiota* s.l. The wall ranges from thin and simple in the tribe *Lepioteae* to thick and complex in the tribe *Leucocoprineae*. In addition, apical wall modifications such as germ pore and truncate apex are used to define tribes, genera and species.

According to Kühner (1972), a thick spore wall is composed of four membranes, as seen under a light microscope. These membranes were recognized after a 12 hour treatment with ammonia-acetic acid and Cresyl blue. A preliminary study, using the same technique, showed that it works only for the species of *Macrolepiota* and few species of *Leucocoprinus*. In other species, the time needs to be reduced to fewer (3-4) hours and in other cases this technique does not work at all. Very often, the basidiospores stain so strongly that no membranes can be recognized.

Kühner (1972, 1980) also described the morphology of the spore wall using Giemsa and iodine.

In the taxonomy of *Lepiota* s. l., one of the most important features of the spore wall is the reaction of the endosporium (the membrane in contact with the cytoplasm) to Cresyl blue. In the species belonging to tribe *Leucocoprineae* the endosporium turns purple (metachromatic reaction) in Cresyl blue. This information however is missing for most types. Based on the results of this reaction, several species need to be transfered from *Lepiota* to either *Leucoagaricus* or *Leucocoprinus*.

Species of *Macrolepiota* and *Chlorophyllum* have thick-walled basidiospores and a conspicuous germ pore. In *Leucocoprinus* and *Leucoagaricus*, basidiospores can be either thin- or thick-walled and they may or may not have a germ pore. *Lepiota* s.s., *Rugosospora*, and *Cystolepiota* are characterized because their basidiospores are rather thin-walled and lack a germ pore.

Except for the genera *Rugosospora*, *Hiatulopsis*, *Januaria*, and *Smithiomyces* (Singer, 1986) and for *Leucoagaricus pulverulentus* Bon (Candusso and Lanzoni, 1990), which are characterized by their ornamented basidiospores, the spore wall of the other genera of

Lepiota s. l. have been described as smooth. However, two Colombian taxa, one belonging to section *Stenosporae* of *Lepiota* s.s. and one belonging to *Leucoagaricus*, are distinctive because of their ornamented basidiospores. This ornamentation is papillate and low verrucose for the latter. One of the examined types, *Lepiota petasiformis* Murrill, has finely echinulate basidiospores.

Germ pore. The germ pore was the first microscopic feature used to split the genus *Lepiota* s. l. Patouillard (1888) created the genus *Leucocoprinus* for those species of *Lepiota* having a germ pore. The presence of a germ pore was one of the features used for the separation of *Lepiota* s.l. into additional groups (Kühner and Romagnesi 1953; Locquin 1956; Smith and Shaffer, 1964). Singer (1949; 1962; 1975; 1986) used its presence or absence at tribal level, to separate the tribe *Leucocoprineae* and *Lepioteae*. However, its use may be confusing because it is not present in all genera belonging to *Leucocoprineae* (e.g. *Rugosospora* and *Sericeomyces*), and it is not constant in all the species belonging to *Leucoagaricus* or *Leucocoprinus*. Thus, I am using it at generic and/or sectional level within the tribe *Leucocoprineae*. A conspicuous germ pore can found in basidiospores of *Chlorophyllum*, *Macrolepiota*, species of *Leucoagaricus* section *Annulati*, and species of *Leucocoprinus* sections

Leucocoprinus and Velutipedes. None of the known species of the genera belonging to the tribe Lepioteae has a germ pore.

During this work I have been able to recognize, under a light microscope, two kinds of germ pores. The first kind (Fig. 2a-b) is represented by a pore present in basidiospores with thick walls and in which a medulla is present. This germ pore is broad and/or very conspicuous. The second kind (Fig. 2c-d) is represented by a pore present in basidiospores in which the spore wall is attenuate apically to the pore and in which no medulla is present.

Based on the reaction of the medulla to Cresyl blue, two subtypes of the first kind are well differentiated. In the first subtype, corresponding to Kühner's first type (Fig. 2a), the medulla hardly stains with Cresyl blue and seems to be a distinctive characteristic of the species of Macrolepiota. In the second subtype, corresponding to Kühner's second type (Fig. 2b), the medulla turns purple with Cresyl blue and is considered as a taxonomic characteristic of some species of Leucoagaricus and some species of Leucocoprinus (Kühner, 1980; Bon, 1981). The second kind of germ pore, corresponding to Kühner's third type, can be broad and conspicuous (Fig. 2c) or it can be formed by the thinness of the spore wall at the apex of the spore (Fig 2d).

Number of nuclei. With few exceptions, the basidiospores of Lepiota s. l. are binucleate. Section Anomalae of Lepiota s.s. and Cystolepiota are charaterized by their uninucleate basidiospores (Candusso and Lanzoni, 1990; Bon, 1981; Kühner, 1980).

Although Knudsen (1978) transferred section Echinatae of Lepiota to Cystolepiota, later Knudsen (1980) retained the section in Lepiota using the number of nuclei of the spore as one of the features to delimit them. However, Knudsen (1980) also pointed out that the difference in the number of nuclei is important but not absolute. He only investigated three species of Cystolepiota. In my work, the number of nuclei of the basidiospores was studied in only one species of Lepiota section Echinatae. Therefore, I am unable to support Knudsen's observations and I have not used this feature taxonomically.

Microchemical reactions. The reactions of the spore wall to Melzer's reagent, Cresyl blue, and ammonia-acetic acid, have been used in the taxonomy of Lepiota s. l., at tribal, generic, and sectional levels.

Reaction to Melzer's reagent. The dextrinoid, amyloid or inamyloid reactions of the basidiospores of Lepiota s. l. in Melzer's reagent were used by Singer (1962, 1975, 1986) at the generic and at the sectional level. According to Singer, the genera Smithiomyces, Chamaemyces, and Hiatulopsis, as well as the species of section Cystolepiota of Cystolepiota and some species of the section Cristatae of Lepiota s.s., have inamyloid basidiospores. Amyloid basidiospores are rare within Lepiota s.l. but they characterize the sections Amyloidae and Amylosporae of Lepiota s.s. The dextrinoid reaction of the basidiospores is more common within Lepiota s.l. All the genera belonging to the tribe Leucocoprineae and the genera and/or sections not mentioned above have dextrinoid basidiospores. Except for the species of Cystolepiota with inamyloid basidiospores, all the Colombian species cited here have dextrinoid basidiospores.

Although the reaction of the basidiospores to Melzer's reagent has been used in taxonomy, and I do support its use at generic and sectional levels, some problems may arise with respect to its interpretation. In this study, especially when examining types, basidiospores that at first were inamyloid, appeared dextrinoid when viewed a few minutes to a few hours after the preparation. In other species, the dextrinoid reaction can be seen only when the basidiospores are in masses; in these cases, single basidiospores appear inamyloid. This reaction also depends on the age of the specimens. In some cases, basidiospores of old collections need to be rehydrated in KOH or ammonia before they are treated with Melzer's reagent. In this work, the species examined that showed a color change to any red or red brown tone in a few, or in many of its basidiospores, were considered as having dextrinoid basidiospores.

Reaction to Cresyl blue. The spore reaction to Cresyl blue is described as metachromatic or not metachromatic. In the metachromatic reaction, the endosporium turns pink to purple when the basidiospores have been placed in aqueous solution of Cresyl blue. This is the reaction of the basidiospores of the species belonging to the genera in the tribe <u>Leucocoprineae</u>. In the "not metachromatic" reaction, the spore remains hyaline or bluish [reaction called orthochromatic (Candusso and Lanzoni, 1990)] in Cresyl blue and is the reaction of the basidiospores of the species belonging to the genera in the tribe <u>Lepioteae</u>.

In my opinion, the spore reaction to Cresyl blue is the most important of the microchemical reactions at the tribal level. However, problems can arise when using it because the intensity of the reaction and the the variability of the reaction time. Nevertheless, very good results can be obtained when the basidiospores are treated first with ammonia and then acetic acid (Kühner, 1972, 1980; Ruini, 1989) for about 5-10 min. in each solution and then placed for 5 min. in Cresyl blue. Increased time in Cresyl blue was used by Kühner (1972) to differentiate the membranes of the spore wall.

Reaction to ammonia and acetic acid. The swelling reaction of the basidiospores to a treatment in 10% ammonia for 5-10 min. and then in 10% acetic acid is recorded as positive when the episporium of the spore distends and negative when there are no changes in the spore wall. The technique was used first by Locquin (Kühner, 1972) and has been applied in the taxonomy of Lepiota s.l. Heinemann (1968) used it as one of the features to separate Chlorophyllum from Macrolepiota. Based on a negative reaction, Bon (1981) pointed out that except for the species of the L. acutesquamosa complex, section Echinatae of Lepiota should be retained in Cystolepiota. The data obtained during this work showed that this character is not constant even at the species level, and probably depends on the age of the basidiospores. Thus, because it is of doubtful taxonomic value this reaction was not used.

Lamellae

Basidia and basidioles. The basidia of Colombian species of Lepiota s. l. are mostly clavate, although pyriform to subpyriform basidia are also found. The size ranges from 12-15 x ±6 μm in Cystolepiota to 46-60 x 15-20 μm in Macrolepiota.

The basidia of the taxa included in this work were mostly 4-sterigmate. However, some of these taxa possess 1-3-sterigmate basidia. In these cases, sterigmata are longer and the basidiospores produced are bigger [e.g. Leucoagaricus hortensis (Murrill) Pegler]. Lepiota bisporigera is a new taxon with 2-sterigmate basidia. Although most species of Lepiota s. l. are described having 4-sterigmate basidia, Leucocoprinus biornatus (Berk. & Br.) Locquin and Leucoagaricus bisporus Heinem., are characterized because their basidia are 2-sterigmate.

Nonetheless, the shape of basidia and number of sterigmata seem to have little taxonomic value. Singer (1949, 1962, 1975, 1986), in distinguishing the species of Leucoagaricus and Leucocoprinus, pointed out the presence of polymorphic basida (Psathyrella-type) and numerous pseudoparaphyses (brachybasidioles, or pavement cells) in Leucocoprinus. On the other hand, Leucoagaricus is characterized by monomorphic basidia (Paneolus-type) and not well-differentiated paraphyses. The same concept has been used by Bon (1981), Smith (1982), and Candusso and Lanzoni (1990). Preliminary data, obtained during this work, showed that paraphyses are well-differentiated in the species of Leucocoprinus with a thin and fragile pileus (e.g L. tenellus, L. fragilissimus, L. cepaestipes). In Leucoagaricus, and in species with rather fleshy basidiomata placed in Leucocoprinus, they resemble young basidia. In addition, in some species with very thin lamellae (e.g. Leucocoprinus tenellus), and in species where the tissue does not revive well basidia are not easy to distinguish and their polymorphic condition is unknown. In this work, polymorphic basidia were found in L. fragilissimus and L. cepaestipes.

Although my observations showed that these two features (paraphyses and/or polymorphic basidia) seem to have taxonomic value in the separation of Leucoagaricus and Leucocoprinus, my data is based on few species and before a final statement is made, information based on other species is necessary. Thus, in this work, these two features are used at species level.

The basidioles or immature basidia are more or less of the same shape but smaller than basidia and have no taxonomic value in *Lepiota* s.l.

Pleurocystidia. Except in the genus *Chamaemyces* and in some species of *Cystolepiota*, the presence of pleurocystidia (cystidia located at the sides of lamellae) are rather uncommon but are important at the species level. Because pleurocystidia are usually scattered and often optically refractive, they can be easily overlooked. The morphology is variable but very distinctive from basidioles. In this work, globose pleurocystidia were found in *Leucocoprinus zamurensis*, mucronate to capitate pleurocystidia were found in *Leucocoprinus sulphurellus* and *Cystolepiota coquisorum* sp. nov., and clavate to ventricose, thick-walled, and incrusted pleurocystidia were found in *Leucoagaricus incrustatus* sp. nov. Pleurocystidia are absent in *Macrolepiota*, *Chlorophyllum*, and *Rugosospora*. Although according to Singer (1986) some species of *Lepiota* s.s. have pleurocystidia, they were not observed in any of the Colombian taxa.

Cheilocystidia. Cheilocystidia are defined as the sterile, differentiated elements located at the edge of lamellae. The edge of a lamella may be sterile and composed entirely of cheilocystidia, or cheilocystidia may be scattered along the fertile lamellar edge. All taxa reported in this work had cheilocystidia. Sizes ranged from 20 x 4 μm in Lepiota bettinae to 80 x 16 in Leucocoprinus cepaestipes. Morphology ranged from cylindrical, clavate, broadly clavate, pyriform, flexuose, utriform, ventricose to ventricose-rostrate. Cheilocystidia are mostly unicellular but at times they are 1-several septate (e.g Macrolepiota colombiana, and Lepiota narinyensis sp. nov.). Although incrusted cheilocystidia are not very common in the group, they were found in two of the Colombian taxa (Leucoagaricus rubrotinctus and Leucoagaricus incrustatus). Bon (1981) also reported incrusted cheilocystidia for Leucocoprinus arenicola, Leucoagaricus serenus and Leucoagaricus purpureorimosus.

Hymenophoral trama. The hyphae forming the lamellar trama of the species of Lepiota s.l. are regularly to subregularly arranged. Modifications of the lamellar trama occur in the species belonging to genera of tribe Leucocoprineae. In these species, the trama which is regular in young specimens and becomes subregular to loosely interwoven with age. This type of trama has been called lacunose (Heinemann, 1989) and is the term used in this work.

The hymenopodium is a layer of filamentous hyphae separating the hymenophoral trama and the subhymenium. The hymenopodium and is not well differentiated as a layer in *Lepiota* s. l. Although Heinemann (in Guzmán, 1992) has suggested its study, it is inconsistent even within the same species and seems not to have taxonomic value. The hymenopodium was mentioned in this work only when it was well defined as a layer (e.g. *Macrolepiota quindiana* sp. nov.).

Subhymenium. The subhymenium of the species of *Lepiota* s. l. is characterized by being cellular or pseudoparenchymatous. The thickness of the subhymenium ranged from 5-10 μm in small species of *Lepiota* s.s., to 25-30 μm in species of *Macrolepiota*. Although it is cellular in appearance in tangential section of lamellae, the cells are not isodiametric and the number of basidia and basidoles that each cell bears vary from 1-2(3), but this is not constant at the species level. Contrary to Heinemann (in Guzmán, 1992), I found that these features of the subhymenium are not very important in the taxonomy of the group.

Pileus

Pileus trama. Hyphae forming the pileus trama in *Lepiota* are parallel to interwoven but radially arranged. Hyphae are usually branched or anastomosed, cylindric to inflated but never pseudoparenchymatous. The hyphal walls are thin and typically non-incrusted in the species included herein; rarely were incrusted hyphae found. The color of the pileus trama ranged from yellowish to hyaline in H_2O and KOH, and the reaction to Melzer's reagent was always inamyloid. With species of Leucoagaricus section Piloselli, the pileus trama turns greenish in NH_4OH.

Pileus surface. The pileus surface in Lepiota s. l. is very variable and has a great taxonomic importance at the generic, sectional and specific levels. In this work, I have adoptedd the terminology used by Bas (1969) which implies location rather than morphology. The term **suprapileipellis** as used in this work refers to the pileus surface that breaks apart leaving an entire center "calotte" and small to large scales toward the margin (e.g. species of Macrolepiota). **Subpileipellis** refers to the layer underneath the suprapileipellis; if an intermediate layer is present it was called **mediopileipellis.** The term **pileipellis** refers to the pileus surface in which only one layer is observed. In this case the pileus surface breaks forming fibrillose to squamulose surface (e.g. Rugosospora).

Microscopically, the morphology of the pileipellis and/or suprapileipellis, as seen in a radial section at the disc of the pileus, of the Colombian taxa fall into any of the following categories: **cutis**, **trichodermium**, **hymenodermium**, and **epithelium** (Bon, 1981; Candusso and Lanzoni, 1990). During this work, I have found that the pileipellis type, together with the spore characters are the most important features in the taxonomy of Lepiota.

Cutis. As used in this work, cutis refers to the pileipellis formed of parallel to interwoven, cylindric, repent hyphae with a radial orientation. The hyphae forming the scales are often semierect at the tips but they do not form a trichodermium. The terminal cells of the hyphae in the cutis-type pileipellis are cylindric, narrowly clavate to broadly clavate. This type of pileipellis is typical in Leucoagaricus and in some species of the sections Ovisporae, Lepiota, and Anomalae of Lepiota s.s.

Trichodermium. A trichodermium refers to a pileipellis formed of erect hyphae arranged perpendicularly to the pileus trama. In the trichodermium-type pileipellis several variations can be observed.

a. Trichodermium formed of a single layer of septate or aseptate hyphae of different lengths characterized by having an acute apex [e.g. Macrolepiota procera (Fig. 8b)]

b. Trichodermium formed of a single layer composed of clavate hyphae of different lengths mixed with cystidioid elements [e.g. *Leucoagaricus zarzalensis* sp. nov. (Fig. 16d)]

c. Trichodermium formed of a single layer of ±catenulate hyphae [e.g. *Macrolepiota colombiana* (Fig. 8a)]

d. Trichodermium formed of cylindric hyphae with globose, non detersile terminal cells (e.g. section *Echinatae* of *Lepiota* s.s).

e. Two layered trichodermium in which the upper layer is formed of cylindric, unicellular or septate hyphae of different lengths, sometimes with cystidia-like elements and a hymeniform basal layer formed of clavate to pyriform elements [e.g. *Leucocoprinus zamurensis* (Fig. 19e).

f. Two layered trichodermium in which the upper layer is formed of long cylindric, unicellular or septate hyphae of different lengths, and the basal layer formed of short hyphae but not forming a hymeniform layer.

Hymenodermium. Defined as the pileipellis formed of elongate, clavate to pyriform hyphae of equal height, arranged perpendicular to the pileus trama. This kind of pileipellis is also frequently referred as hymeniform and has a peudoparenchymatous appearance in scalp section. At the generic level, a hymeniform pileipellis is found in *Chamaemyces* (not found in Colombia) and in *Rugosospora*. It also differentiates the sections *Cristatae* and *Lilaceae* of *Lepiota* s.s. At the species level a hymenodermium is present in *Macrolepiota* *rachodes*. In a tangential section of a hymeniform suprapileipellis (e.g.*Lepiota* *cristata*, and *L.* *rubiginosoides*) a second layer with pseudoparenchymatous appearance formed of non isodiametric cells can be observed. In an extralimital collection at PC, determined as *L.* *carminee* (nomen nudum) three-well defined layers form the suprapileipellis. The first layer in contact with the environment is hymeniform, the second layer is formed of a pseudoparenchymatous tissue, and the third layer, in contact with the subpileipellis, is hymeniform.

Epithelium. This is considered as a pileipellis formed of a single layer of loose, subglobose to globose cells. These cells rise from the repent hyphae forming the subpileipellis but easily detach from them. This pileipellis is said to be the universal veil (Kühner, 1980) and gives a granulose to pruinose macroscopic appearance. It is found in species of *Cystolepiota* and some *Leucocoprinus* spp.

Stipe

Stipe context. The stipe context of all species of Lepiota studied are formed of cylindric cell which are parallel and vertically oriented. The stipe context has no taxonomic value and is not included in the descriptions in this work.

Stipe surface. Since the stipe surface of the Colombian species of Lepiota s.l. included here are formed of one single layer, I refer to it as a **stipitipellis.** Although the stipitipellis morphology is missing for most descriptions of Lepiota s. l., it may have an important taxonomic value at the species level and may help to define sections, but information on more taxa is needed.

Stipitipellis. The stipitipellis of several species is formed of cylindric, parallel to vertically oriented hyphae, with no traces of the tissue forming the pileipellis observed in this layer (e. g. Leucoagicus rubrotinctus, Lepiota cristata, and most species of section Ovisporae, and Anomalae of Lepiota s.s.).

However, in some species, the stipitipellis is formed of cylindric, parallel to slightly interwoven hyphae with vertical orientation, and which give rise to tufts of hyphae similar to the hyphae forming the pileipellis tissue.

In other species, the stipitipellis is characterized by being a continuation of the pileipellis (e.g. Macrolepiota colombiana, Leucoagaricus zarzalensis, and most of the species belonging to section Stenosporae of Lepiota s.s.). This is the case, agree with Fries' (1821) and Atkinson's (1814) definition of Lepiota as having an universal veil concrescent with the pellis of pileus and stipe.

Veils

Universal veil. The universal veil of Lepiota s.l. was described as being concrescent to the pileus epicutis by Fries (1821). I found however that in Macrolepiota colombiana and Lepiota hemisclera (not included in this work) the universal veil and the pileipellis form two layers that are microscopically different. Based on an ontogenetic study, Atkinson (1914) pointed out that the universal veil of Lepiota clypeolaria becomes concrescent with the pileus and stipe surfaces. In this species, the pileipellis and the stipitipellis share the same kind of tissue. Similarly the pileipellis and the stipitipellis of some species of Lepiota s.l. (Macrolepiota colombiana, Leucoagaricus zarzalensis, and Lepiota erythrosticta, among others) share the same kind of tissue, however there are not enough studies to prove that it is the universal veil and not the epicutis itself which gives the final morphology of the pileipellis and stipitipellis. In this work, unless remnants of a universal veil were well defined, I did not refer to them. Thus, the terms pileipellis and stipitipellis as used, may or may not include the universal veil.

Partial veil. In this work, the microscopic description of the partial veil was based on longitudinal sections. The inner side of the annulus corresponds to the part of the annulus that developed (Fig. 3b) facing the hymenium; the outer side of the annulus corresponds to the side that developed in contact with the stipe during primordial stages (Fig. 3c). Free edge refers to the edge that was attached to the margin of the pileus (Fig. 3a) and the lower edge refers to the edge that remains attached to the stipe (Fig. 3d).

The inner side of the annulus, is usually formed of cylindric hyphae which are parallel to interwoven and radially oriented. In one species (Leucoagaricus zarzalensis), these hyphae give rise to scanty tufts of hyphae similar to those forming the pileipellis.

If pileipellis tissue passes into the stipe, then the outer side of the annulus is formed of hyphae similar to those forming the pileipellis (e.g. species of Macrolepiota colombiana, M. procera, Chlorophyllum molybdites). If the stipitipellis and the pileipellis do not share the same kind of tissue, then the tissue of the outer side of the annulus is similar to the tissue forming the stipitipellis.

In some species (e.g. Leucoagaricus rubrotinctus and Lepiota guatopoensis), the annulus at its free edge is formed of hyphae similar to those forming the pileipellis and the rest of the annulus is formed of hyphae similar to the stipitipellis. In one species not included in this work (Lepiota hemisclera), only the tissue at the lower edge of the annulus is similar to the tissue forming the pileipellis, the rest of the annulus is formed of hyphae interwoven with no definite orientation.

Until now, only the macroscopic appearance of the annulus has been considered taxonomically. However, I think that the microscopic features of the annulus are useful at least at the specific level. For example, the presence of hyphae similar to those forming the pileipellis in the inner side of the annulus of Leucoagaricus zarzalensis are absent in close related species (e. g. Lepiota americana Peck).

Clamp connections

The presence of clamp connections was used by Singer (1949, 1962) at the generic level to separate Macrolepiota from Chlorophyllum. However, clamp connections in Chlorophyllum were reported later by Sundberg (1968).

Singer (1986) also used the presence of clamp connections in Macrolepiota to separate it from Leucoagaricus, but I have found that some species belonging to Leucoagaricus have clamp connections (e.g. L. naucinus). Furthermore, Heinemann (1977) reported clamp connections in L. bisporus and Pegler (1983) reported them in L. hortensis.

In most type descriptions, clamp connections were not reported when present only on the stipe. In this work clamp connections were considered important at sectional and specific level.

CHAPTER IV

Taxonomic treatment

Agaricaceae Cohn

Hedwigia 11: 17. 1872.

Type genus: Agaricus L.:Fr.

Basidiocarp pluteoid or lepiotoid, ranging from small and very fragile to large and robust, fleshy and putrescent. Pileus convex, umbonate to plane; pileus surface glabrous to squamulose. Context sometimes showing color changes when bruised. Lamellae free. Stipe central, cylindric to bulbous; stipe surface glabrous, fibrillose or similar to the pileus surface. Annulus generally present but sometimes absent. Spore print variable from pure white, green, or brown. Spores ovoid, ellipsoid, fusoid, or sometimes spurred; spore wall simple to complex, smooth or ornamented; germ pore present or absent; inamyloid, amyloid or dextrinoid in Melzer's reagent, metachromatic or not in Cresyl blue. Hymenophoral trama regular, irregular, sometimes lacunose but never bilateral. Pileipellis very variable, repent, trichodermal, hymeniform, epithelial or formed of chains or loose sphaerocysts. Clamp connections present or absent.

Key to tribes

1. Spores metachromatic in cresyl blue; dextrinoid in Melzer's reagent; germ pore broad and conspicuous but sometimes absent; spore print white, sometimes green but never brown or sepia; lamellae free................ _Leucocoprineae_, p. 73

1. Spores not metachromatic in Cresyl blue; dextrinoid or inamyloid in Melzer's reagent; spore print, if white, spores without germ pore or if brown or sepia, spores may or not have germ pore; lamellae free.

    2. Spore print brown or sepia .... _Agariceae_ (Not included in this work)

    2. Spore print white, cream, pinkish, yellowish........ _Lepioteae_, p. 75

Tribe _Leucocoprineae_ Singer, Pap. Michigan Acad. Sci. 32: 141. 1948.

Type genus: _Leucocoprinus_ Pat.

Basidiomata medium to large, lamellae free, often collariate. Annulus present, often evanescent, often moveable. Spore print white to whitish but also green. Basidiospores ovoid, ellipsoid to oblong, dextrinoid in Melzer's reagent, always metachromatic in Cresyl blue; germ pore present or absent; spore wall thin to complex, smooth or ornamented. Clamp connections present or absent.

Key to genera found in Colombia

1. Spore print white to pale cream; basidiomata various; volva present or rudimentary.

    2. Basidiomata very large; annulus double and moveable; clamp connections present; volva, if present, rudimentary .... <u>Macrolepiota</u>, p. 84

    2. Basidiomata small to medium; annulus simple, membranous, often evanescent; clamp connections present or absent; volva absent.

        3. Clamp connection present; spores rugulose to reticulate; germ pore absent; pileipellis

hymeniform..
Rugosospora, p. 138

3. Clamp connections absent; spores rarely ornamented; germ pore present or absent; pileipellis various.

4. Basidiomata ±thick and fleshy; pileal margin not striate...................................
Leucoagaricus, p. 96

4. Basidiomata slender or very fragile; pileal margin sulcate striate........................
Leucocoprinus, p. 118

1. Spore print green, basidiocarp large and robust; volva absent..
Chlorophyllum, p. 78

Tribe Lepioteae Fayod, Prodrome, Ann. Sc. Nat. Bot. VII. 9: 349. 1889.

Type genus: Lepiota (Pers.) Fr.:S. F. Gray

Basidiomata tiny to medium size, lamellae free. Annulus present, membranous, fibrillose, to arachnoid, often evanescent. Spore print white to creamy; basidiospores broadly ellipsoid to fusiform or sometimes spurred but never globose, inamyloid, dextrinoid or amyloid in Melzer's reagent, never metachromatic in Cresyl blue; without germ pore; spore wall simple, smooth, rarely ornamented. Clamp connections absent or present.

Key to genera found in Colombia

1. Pileipellis an epithelium, formed of loose sphaerocysts; pileus surface finely granulose, pulverulent to squamulose................................ <u>Cystolepiota</u>, p. 145

1. Pileipellis variable, a cutis, a trichodermium or hymeniform, but never an epithelium or with loose sphaerocysts; pileus surface matted fibrillose, scaly-fibrillose, fibrillose, squamulose, rarely glabrous.. <u>Lepiota</u>, p. 149

Chlorophyllum Massee

Bull. Misc. Inform. 1898: 135. 1898.

Type species: *Chlorophyllum esculentum* Massee [*C. molybdites* (Meyer: Fr.) Massee]

The genus was created by Massee as analogous to *Lepiota* but distinguished by the green lamellae and basidiospores. Macroscopically, the genus is characterized by having large, lepiotoid basidiomata in which the surface of the pileus breaks up leaving an entire center and large plate-like scales toward the margin. The context of the pileus and stipe stain reddish when exposed. The lamellae are free, separated from the stipe by a well-developed collarium, white when young and green when mature. In addition, the stipe is central, bulbous, and annulate. The annulus is double and becomes moveable with age. Microscopically, the genus lacks pleurocystidia; basidiospores are smooth with a complex thick wall, and possesses a broad germ pore; the spore wall does not stain with Congo red in alkali mounts (Weresub, 1971; Singer, 1975; 1986), and does not distend when treated with ammonia and acetic acid (Heinemann, 1968). Clamp connections are present.

Chlorophyllum molybdites (Meyer:Fr.) Massee, Bull. Misc. Inform. 1898: 136. 1898.

Figs. 4, 5a-e.

≡ Agaricus molybdites Meyer:Fr., Syst. Mycol. 1: 308. 1821.

≡ Lepiota molybdites (Meyer: Fr.) Sacc., Syll. Fung. 5: 30. 1887.

≡ Mastocephalus molybdites (Meyer:Fr.) Kuntze, Rev. Gen. Pl. 2: 860. 1891.

≡ Leucocoprinus molybdites (Meyer:Fr.) Pat., Bull. Soc. Mycol. France 29: 215. 1913.

= Agaricus morganii Peck, Bot. Gaz. (Crawfordsville) 4: 137. 1879.

≡ Lepiota morganii (Peck) Sacc., Syll. Fung. 5: 31. 1887

≡ Mastocephalus morganii (Peck) Kuntze, Rev. Gen. 2: 860. 1891.

≡ Chlorophyllum morganii (Peck) Massee, Bull. Misc. Inform. 1898: 136. 1898.

= Agaricus glaziovii Berk., Vidensk. Meddel. 1879-80: 32. 1880

≡ Pholiota glaziovii (Berk.) Sacc., Syll. Fung. 5: 751. 1887.

= Lepiota ochrospora Cooke and Massee, Grevillea 21:

73. 1893.

= _Chlorophyllum_ _esculentum_ Massee, Bull. Misc. Inform. 1898: 136. 1898.

≡ _Lepiota_ _esculenta_ (Massee) Sacc. and Syd., Syll. Fung. 16: 2. 1901.

= _Agaricus_ _guadelupensis_ Pat., Bull. Soc. Mycol. France 15: 197. 1899.

= _Annularia_ _camporum_ Speg., Anales Mus. Nac. Buenos Aires 6: 117. 1899.

≡ _Lepiota_ _camporum_ (Speg.) Speg., Bol. Acad. Nac. Ci. 29: 114. 1926.

= _Agaricus_ _congolensis_ Beeli, Bull. Soc. Roy. Bot. Belgique 61: 92. 1928.

≡ _Chlorophyllum_ _molybdites_ (Meyer:Fr.) var. _congolensis_ (Beeli) Heinem., Fl. Icon. Champ. Congo 16: 323. 1967.

Pileus 6-18 cm diam, convex, plane to umbonate; surface dry, not hygrophanous; surface brown (6F8, 7F8) to vinaceous (9F8), completely entire in young basidiomata, entire at the center, breaking into small to large scales on whitish background toward the margin with age; margin inrolled to decurved, entire. Context up to 2 cm thick, white, changing to reddish brown (8B3) when exposed. Odor pleasant, taste not distinctive to sweet. Lamellae free, separate from the stipe by a collarium, close, up to 1.5

cm broad, white to yellowish white (paler than 4A2) when young, becoming greenish to green-brown with age, often staining reddish when bruised; margin entire to eroded, not marginate. Stipe 10-20 cm long, up to 2.5 cm wide, central, bulbous, separable from pileus; surface smooth at the apex, finely fibrillose below the annulus, whitish at first then gray brown to dark brown, annulate. Annulus superior, double, becoming moveable, whitish on the inner side, concolorous with epicutis of pileus outside.

Macrochemical tests: positive for tyrosinase; negative for laccase.

Basidiospores (Fig. 5a) greenish-brown (4B3) to olive brown (4E5) in mass, 9-11 x 6.5-8(9) μm ($\overline{Q}$ = 1.4), ovoid to amygdaliform in all views, apically truncate by a broad germ pore, hyaline in KOH, dextrinoid in Melzer's reagent, metachromatic in Cresyl blue; spore wall thick, smooth. Basidia (Fig. 5b) clavate to narrowly clavate, 4-sterigmate, hyaline, inamyloid, 30-40 x 8-10(12) μm. Pleurocystidia absent. Edge of lamellae with crowded cheilocystidia and scattered basidia. Cheilocystidia (Fig. 5c) abundant, pyriform to sphaeropedunculate, 30-45(52) x 14-20 μm. Hymenophoral trama regular at first, becoming lacunose with age; hyphae cylindric, hyaline to greenish in KOH, 6-12(20) μm broad. Hymenopodium often well defined, formed of hyphae 3-8 µm broad. Subhymenium pseudoparenchymatous, up to 20 µm thick; with cells 4-15 µm diam. Pileus trama (Fig. 5e) hyaline to yellowish in KOH, formed of densely interwoven hyphae; hyphae 7-14(20) µm broad. Subpileipellis yellowish brown in KOH, formed of densely interwoven hyphae which give rise to a suprapileipellis formed of an intricate trichodermium (Fig. 5d0. Hyphae of the suprapileipellis tightly packed, with cylindric to clavate terminal cells; terminal cells 8-10(12) µm broad. Stipitipellis hyaline to yellowish in KOH, composed of parallel and vertically oriented hyphae; hyphae thin-walled, (2)3-9 µm broad. Annulus on its inner side formed of hyphae loosely interwoven but vertically oriented as seen in longitudinal section, hyaline to yellowish in KOH; the outer side is formed of densely interwoven hyphae similar to those forming the suprapileipellis. Clamp connections rare throughout the basidioma..

Material studied: COLOMBIA. DPTO. ANTIOQUIA: Mpio. de Envigado, Urbanización Alqueria de San Isidro, 29 May 1992, Franco-M. 892 (HUA, NY); Mpio. de Medellín, a la entrada de la Fábrica de Licores de Antioquia, 29 May 1992, Franco-M. 891 (HUA, NY); DPTO. VALLE: Mpio. de Cali, Universidad del Valle (Melendez), between the administration building and the Central Library, lawn cultivated trees, 976 m, 4 Nov. 1987, P. Silverstone 3352 (CUVC, NY); Mpio. de Cali, potreros del Club de empleados de UniValle, 980 m, 5 May 1990, Franco-M. 414 (CUVC, NY). USA. FLORIDA: Duval Co., Jacksonville, I-10 and I-15 junction, on lawn at Holiday Inn, 8 Aug 1985, R. E. Halling 4499 (NY).

Distribution: Cosmopolitan, tropical America, Oceania, Asia, North America (Florida to New York, California, and Michigan), south to Buenos Aires (Singer, 1986). In Colombia, it has been collected in Antioquia and Valle.

Discussion: Although Heinemann (1968) recognizes three species based on spore size and shape, the genus is considered monotypic by most authors. Chlorophyllum differs from Macrolepiota by having green basidiospores and from Clarkeinda by lacking a volva. The dark green color of the spores in KOH, and the negative reactions of the spores to Congo red and ammonia-acetic acid further separate Chlorophyllum from Macrolepiota. However, since some basidiospores of Macrolepiota take a few minutes before staining with Congo red, and the spore wall of some basidiospores of Chlorophyllum distend in ammonia-acetic acid treatment, it is necesary to use these characters in conjunction with the color of the basidiospores of mature basidiomata for an accurate determination. The presence of clamp connections can be found as an inconstant character in both genera and is not a reliable character for separating them. According to Sundberg (1971), *Chlorophyllum molybdites* differs from *Macrolepiota rachodes* (Vitt.) Quél. in the structure of the suprapileipellis; the latter species possesses a palisade of pyriform cells at the disc.

Macrolepiota Singer

Pap. Michigan Acad. Sci. 32: 141. 1948.

Type species: Lepiota procera (Scop.: Fr.) S. F. Gray [Macrolepiota procera (Scop.: Fr.) Sing.]

The genus was created by Singer to include species with big (above 10 µm length), metachromatic basidiospores, white spore print, and having clamp connections. Macroscopically, the carpophores are characterized by being tall, possesing lamellae separated from the stipe by a well developed collarium, and having a complex annulus which becomes moveable with age. In addition, the context of the pileus and stipe become reddish when bruised (Romagnesi, 1990). Microscopically, the genus lacks pleurocystia, and the hymenophoral trama becomes lacunose with age (Heinemann, 1989), and the ultrastructure of the spore wall consists of a double episporium and a metachromatic endosporium (Romagnesi, 1990). Chlorophyllum differs from Macrolepiota in the green spore print, in lacking or very inconstant clamp connections, and in the reaction of the basidiospores to Congo red. The spores of Chlorophyllum do not stain with Congo red while the spores of Macrolepiota become red to orange (Weresub, 1971). Furthermore, the basidiospores of Chlorophyllum are not affected by treatment with ammonia and acetic acid, while the basidiospores of *Macrolepiota* distend under the same treatment (Heinemann, 1968). *Leucoagaricus* also lacks clamp connections (Singer, 1986) and lacks a well-developed germ pore (Heinemann, 1969).

Key to species found in Colombia

1. Basidiospores ellipsoid to ovoid with rounded apex, with an evident apical germ pore.

    2. Epicutis of pileus breaking up into large plate-like squamules on fibrillose background; suprapileipellis trichodermial, formed of very long, thin hyphae with acute apices...
    M. procera (Scop.: Fr.) S. F. Gray (extralimital)

    2. Epicutis of pileus breaking up into small to large plate-like squamules on glabrous background; Suprapileipellis trichodermial, formed of short, catenulate hyphae with rounded apices..............
    M. colombiana, p. 86

1. Basidiospores ellipsoid to amygdaliform, with the apex slightly to strongly truncated by a germ pore:

3. Basidiospores 17-20 x 8-11 µm; context turning vinaceous when exposed..............................
M. quindiana, p. 91

3. Basidiospores 8.5-12 x 6-7 µm; context turning orange or reddish when exposed.....................
M. rachodes (Vitt.) Singer (extralimital)

Macrolepiota colombiana Franco-Molano, sp. nov.

Macrolepiota procerae (Scop.: Fr.) Singer arcte affinis sed epicute in umbonem integram vel subareolatum apicalem et squamules seu areolas, minutas majoresque, submarginales (nec in umbonem centralem et squamas magnas detersiles) diffracta carnem albam laeven vel fibrillosam (nec brum neam fibrilloso-squamulosam) praebenti diversa; ulterius trichodermio e hyphis ±catenulatis 100 µm haud excedentibus (nec cylindricis acutis septatis 300-400 x 8-14 µm) constanti et basidiosporis 12-14(18) x 7-10(12) µm (nec 13-17(23) x (8.5)9-10.5(12) µm a M. procera divergens.

Etymology: Named for the Republic of Colombia.

FIGS. 6, 7a-d.

Pileus 4-12 cm diam, convex, plane to umbonate; surface dry, entire at the center, breaking into large to small scales or areolae to fine granules toward the margin; center and areolae brown (7E7) on white background; margin entire or splitting radially toward the center, tuberculate, inrolled. Context ±5 mm thick, white, slowly changing to greyish-red (7B3) when exposed. Odor very strong of cabbage, taste indistinct. Lamellae free, close, thick, ±1.2 cm broad, white, unchanging; margin finely serrate, not marginate. Stipe 15 cm long, 1 cm broad near the apex, 1.3 cm broad at the middle, 3 cm at the base, central, bulbous, tough, strict to curved; surface dry, smooth to rugulose, glabrous to finely velutinous with a lens, brown (paler than 6F6) except at the base which is white, breaking circumferentially as the stipe elongates, showing a white context; interior white slowly becoming greyish-red (7B3) when exposed, hollow at the center, annulate. Scattered, white, cottony mycelium at the base. Annulus superior, flaring, double, white and membranous on the inner side, tough and concolorous with the stipe outside, becoming moveable with age.

Macrochemical tests: positive for tyrosinase throughout basidiomata; negative for laccase; KOH on pileus, negative.

Basidiospores (Fig. 7b) white in mass, 12-14(18) x 7-10(12) µm ($\overline{Q}$ = 1.56), broadly ellipsoid to ovoid in all views, hyaline in KOH, dextrinoid in Melzer's reagent, metachromatic in Cresyl blue, smooth, thick-walled, with broad germ pore, round at apex. Basidia (Fig. 7a) clavate, narrowly clavate to pedicellate, 4-sterigmate, hyaline in H_2O and KOH, inamyloid, 45-55 (60) x 12-15 µm, often buried in the subhymenium. Pleurocystidia absent. Edge of lamellae sterile with crowded cheilocystidia. Cheilocystidia (Fig. 7c) abundant, oblong to clavate, rarely utriform, mostly septate, often branched; terminal cells 17-55(70) x 8-14 µm. Hymenophoral trama hyaline, inamyloid, lacunose; hyphae cylindric, 3-12 µm broad. Subhymenium pseudoparenchymatous, 25-30 µm thick, formed of cells 2-7 µm diam. Pileus trama hyaline, inamyloid, formed of densely interwoven hyphae; hyphae 4-12(15) µm broad. Suprapileipellis formed of two layers: a basal layer of repent, parallel to loosely interwoven but radially arranged hyphae; hyphae yellowish brown in H_2O, paler in KOH, smooth to slightly incrusted, rather thin-walled, 4-12 µm broad; the basal layer or mediopileipellis giving rise to a trichodermium of hyphae somewhat gelatinized, yellowish brown in KOH, ± catenulate, smooth or incrustated, rather thin-walled, 70-110 x (3)5-12 µm broad (Fig. 7d). Subpileipellis hyaline to very pale yellow in H_2O and KOH, formed of repent, parallel, radially arranged hyphae; hyphae smooth to incrusted, thin-walled, 4-8 µm broad. Stipitipellis formed of parallel to loosely interwoven hyphae but vertically arranged; hyphae similar to those forming the suprapileipellis, yellowish brown in H_2O and KOH, catenulate, smooth, rather thin-walled, 5-15 µm broad. Annulus two layered; the inner layer formed of densely interwoven, hyaline hyphae, 3-10 µm broad; the outer layer is formed for hyphae similar to those forming the stipitipellis. Clamp connections present.

Material studied: Macrolepiota colombiana. COLOMBIA. DPTO. ANTIOQUIA: Mpio. de San Cristóbal, Vereda San José, mixed forest with Pinus and Eucalyptus, ±1700 m, 3 Jun 1992, Franco-M. 913 (HUA, NY); DPTO. BOYACA: Bojirca sector Manzanos, 2800 m, sobre pasto a borde de carretera, 26 Apr 1992, Franco-M. 784 (COL, NY); DPTO. CUNDINAMARCA: Mpio. de Cogua, Parque Neusa, bosque de Pinaceae con predominancia de Pinus patula, 3000 m, 26 May 1991, Franco-M. 694 (HOLOTYPE, COL; ISOTYPE, NY); Between Susa and Simijaca, Finca Taquira, 5°28′ N 73° 51′ W, plantation of Pinus radiata and Pinus patula, in duff, ca 2650 m, 10 May 1987, G. Mueller 2800 (F); NW of Pacho, 5°9′ N 74°9′ W, Quercus humboltii dominated forest, in grass under Quercus humboltii, ca 2450-2500 m, 11 may 1987, G. Mueller 2806 (F); DPTO. NARINO: Mpio. La Florida a 26-28 km de Pasto, hacienda El Barranco, propiedad de Francisco Villareal, sobre pasto a las afueras de bosque de *Quercus humboltii*, 11 May 1990, *Franco-M.* *450* (NY, PSO).

Comparative material examined of *Macrolepiota* *procera*. GERMANY. BAVARIA: Regensburg, Penkertal, between Endfeld and Pen, under *Fagus*, 4 Sep 1990, *Franco-M.* *539* (NY); USA. MASSACHUSETTS: Hampshire Co., Amherst, Wildwood Cemetery, under mixed hardwoods, 18 Sep 1981, *R.* *E.* *Halling* *3437* (NY); NEW YORK: Suffolk Co., Hither Hills State Park, 19 Sep 1965, *C.* *T.* *Rogerson* (NY). PENNSYLVANIA: Butler Co., 5 mi N of Zelienople, 8 Nov 1935, *L.* *K.* *Henry* *369* (NY); SOUTH CAROLINA: Oconee State Park, 18 Aug 1992, *Franco-M.* *1024* (NY).

Distribution: Probably neotropical. It has been collected only in Colombia in the Departamentos of Antioquia, Boyacá, Cundinamarca and Nariño.

Discussion: Apparently because of its size this species has been misdetermined as *Macrolepiota* *procera*. Comparison of fresh collections of both species showed macroscopic differences. In *M.* *procera* the epicutis breaks leaving a "calotte" at the center and small to big detersile scales toward the margin on a brownish, fibrillose to squamulose background while in *M.* *colombiana* the epicutis breaks leaving an entire to finely areolate "calotte" at the center and large or small to tiny appressed scales or areolae toward the margin on a pure white, smooth or finely fibrillose background. Microscopically, the suprapileipellis of M. procera (Fig. 8b) is characterized by a trichodermium formed of long, cylindric, septate hyphae, with acute apices, 300-400 x 8-14 µm (Candusso and Lanzoni, 1992). In M. colombiana, the trichodermiun (Fig. 8a) is formed of ±catenulate hyphae not exceeding 110 µm in length. The subpileipellis of M. procera is bright yellow in KOH while in M. colombiana it is hyaline to very pale yellow. The basidiospores are larger [13-17(23) x (8.5)9-10.5(12) µm] in M. procera, and shorter [12-14 (18) x 7-10 (12) µm] in M. colombiana. Although, septate cheilocystidia can be found in both species, they are more abundant and frequently branched in M. colombiana.

Macrolepiota colombiana resembles M. gracilenta (Krombh.) Moser from which it differs in having bigger basidiospores, 9.8--11.5-7.4-8.4 in the later, and in the size and shape of the cheilocystidia. Macralepiota gracilenta has clavate to pyriform, aseptate cheilocytidia, while M. colombiana has oblong to clavate, rarely utriform, mostly septate, often branched cheilocystidia.

Macrolepiota quindiana Franco-Molano, sp. nov.

Macrolepiota africanae (Heim) Heinemann arcte affinis sed basidiosporis majoribus, cheilocystidiis majoribus et elementis pileocystoideis nullis diversa, ulterius fibulis raris tantum intra stipitem sitis notabilis.

Etymology: Named for the Department of Quindio, Colombia.

FIGS. 9a-f.

Pileus up to 18 cm diam, convex, plane to umbonate; surface dry, dark brown, entire at the center, breaking into large appressed scales toward the margin on light brown, glabrous to finely fibrillose scaly background; margin entire, inrolled. Context thick, white, becoming vinaceous when bruised. Odor and taste not recorded. Lamellae free, close, white, becoming vinaceous when bruised; margin serrate. Stipe up to 30 cm long, ±1 cm wide, central, bulbous; surface fibrillose scaly, whitish at the apex, light brown to brown toward the base, staining vinaceous when handled, annulate. Annulus superior, membranous, dark brown outside, light brown inside.

Macrochemical tests: not performed.

Basidiospores (Fig. 9a) very light brown in mass, (14)17-20(23) x 8-11(15) µm ($\overline{Q} = 1.71$), abnormal basidiospores can reach up to 35 µm long, ovoid, oblong to cylindric with truncate apex in all views, hyaline in KOH, dextrinoid in Melzer's reagent, metachromatic in Cresyl blue; spore wall thick, smooth. Basidia (Fig. 9b) clavate, 4-sterigmate, hyaline, inamyloid, 46-56(60) x 15-19 µm. Pleurocystidia absent. Edge of lamellae sterile with crowded cheilocystidia. Cheilocystidia (Fig. 9c) abundant, clavate to pyriform, (25)35-48 x (10)15-18. Hymenophoral trama hyaline, inamyloid, lacunose, with hyphae (5)7-15 µm broad, thin-walled. Subhymenium ramose, up to 20 µm thick. Pileus trama hyaline, inamyloid, formed of interwoven hyphae but with radial orientation; hyphae 7-10 µm broad, thin-walled. Suprapileipellis (Fig. 9d) formed of densely interwoven hyphae giving rise to an intricate trichodermium; hyphae with dense yellowish brown content in H_2O and KOH, 3-7(10) µm broad. Subpileipellis (Fig. 9e) formed of repent to semierect, densely interwoven hyphae; hyphae with yellowish brown content in H_2O and KOH, 7-10 µm broad. Stipitipellis at the apex of the stipe formed of hyphae parallel and vertically oriented; hyphae with yellowish content in KOH, 4-6 µm broad. Stipitipellis below the annulus formed of hyphae parallel and vertically oriented; hyphae hyaline, 6-10 µm broad, given rise to a tufts of hyphae similar to those of subpileipellis. Annulus formed of densely interwoven hyphae (Fig. 9f); hyphae with yellowish brown content, 4-10 µm broad, thin-walled, similar to those forming the subpellis of pileus. Clamp connections rare on the stipe.

Material studied: COLOMBIA. DPTO. QUINDIO, Mpio. de Salento, camino a la estación La Marina, Alto Quindio, 2800 m, 10 May 1990, R. Bernal 1856 (HOLOTYPE, COL; ISOTYPE, NY); Mpio. de Salento, Estación La Montaña, Alto Quindio, sobre hojarasca en bosque de aliso, 2900 m, 2 Nov. 1990, A. Peñuela y R. Bernal 328 (COL, NY).

Distribution: It has been found only in Colombia in the Departamento of Quindio.

Discussion: Although the clamp connections of this species are rare and they can be found only on the stipe tissue, it is best placed in Macrolepiota because its basidiospores have a complex wall and possess a germ pore. In addition, it possesses the macroscopic characteristics of Macrolepiota. The size of the basidiospores, the size of the basidia, and the lack of pileocystidiod elements differentiate this species from M. africana (Heim) Heinemann. The color change from white to vinaceous of the pileus, stipe and lamellae, the size of the basidiospores, the size of the basidia, and the dense, yellowish brown content of the hyphae forming the pellis of the stipe and pileus appear in this species in a combination not described before.

Leucoagaricus (Locquin) Singer

Sydowia 2: 35. 1948

Leucocoprinus Pat. subg. *Leucoagaricus* Locquin, Bull. Soc. Linn. Lyon 12: 91. 1943

Type species: *Leucocoprinus macrorhizus* Locq. [= *Leucoagaricus macrorhizus* (Locq.) Singer)]

Macroscopically the genus is characterized by having ±small to medium basidiomata with lepiotoid habit. Pileus thick and fleshy; surface radially fibrillose, floccose, squamulose to fibrillose scaly, rarely ±granulose; margin entire or very short striate. Context thick, staining or not when bruised. Lamellae free, rarely collariate. Stipe central, equal to bulbous. Annulus membranous, ±persistent, sometimes moveable. Spore print white. Microscopically, the basidiospores are characterized by having or not having a rudimentary, rarely distinctive, germ pore, and metachromatic endosporium; spore wall rather thin, smooth to ornamented. The hymenophoral trama is regular to lacunose. Pileipellis is variable; it can be a trichodermium or very often a cutis of repent radially arranged hyphae, lacking sphaerocysts. Pleurocystidia sometimes present. Cheilocystidia abundant. Clamp connections absent, very rarely present and if so, usually on the stipe.

Key species found in Colombia

1. Germ pore absent or rudimentary.

   2. Spore wall smooth.

      3. Basidiomata not changing color with NH_4OH.

         4. Pileus surface white, whitish to yellowish; basidiospores 9-11(12.5) x 6-7 µm, ovoid broadly ellipsoid to oblong; basidia 2-sterigmate; pleurocystidia absent; clamp connections present.............................. _L. hortensis_, p. 99

         4. Pileus surface reddish, dark red, grey-orange to orange; basidiospores 5.4-7.2 x 2.7-4.5 µm, ovoid to amygdaliform with acute apex; basidia 4-sterigmate; pleurocystidia present or absent; clamp connections absent.

            5. Pileus 2-3.5 cm diam, dark red; basidiospores 6.3-7.2 x 3.6-4.5 µm, ovoid

to amygdaliform with acute apex; pleurocystidia absent; cheilocystidia abundant, sometimes incrusted, thin-walled.
L. rubrotinctus, p. 102

5. Pileus up to 2 cm diam, grey-orange to orange; basidiospores 5.4-6.3 x 2.7-3.6 μm, ovoid to amygdaliform with acute apex; pleurocystidia and cheilocystidia abundant, apically incrustated, and thick-walled....
L. incrustatus, p. 106

3. Basidiomata turning greenish with 10% NH_4OH; pileus surface reddish brown becoming darker, then black when bruised; lamellae white becoming red when bruised; edge of lamellae brown becoming green-gray when bruised; basidiospores 6-8 x 4-5 μm, broadly ellipsoid to ovoid..................
L. zarzalensis, p. 109

2. Spore wall finely verrucose.

6. Basidiospores 6-8 x 3-4 μm, ellipsoid to subcylindrical; cheilocystidia abundant.
L. guachacanus, 113

6. Basidiospores 4-4.8 x 2.2-2.5 µm, ellipsoid; cheilocystidia absent............
L. pulverulentus (Huijsman) Bon (extralimital)

1. Germ pore broad......................................
Species not known from Colombia

Leucoagaricus hortensis (Murrill) Pegler, Kew Bull., add. ser. 9: 414-415. 1983.

FIGS. 10, 11a-d.

≡ *Lepiota hortensis* Murrill, North Amer. Fl. 10: 59. 1914.

Pileus 3-4(8) cm broad, conic, campanulate to umbonate; surface dry to slightly viscid when wet, white to yellow (5C4), entire at the center and forming small to large appressed scales toward the margin showing a white background; margin pectinate (3-4 mm from margin to center), splitting radially with the expansion of the pileus. Context ±4 mm thick, white, staining reddish orange (7B6). Odor sweet, taste not recorded. Lamellae free, close to crowded, ±6 mm broad, white; margin entire, not marginate. Stipe up to 10 cm long, 4-5 mm wide, central, equal to slightly bulbous; surface glabrous to finely fibrillose, white at the apex, orange grey (near 5B2) below, annulate; interior hollow, white, becoming reddish orange (7B6) when exposed. Annulus superior, membranous, double, concolorous with the stipe, fixed in young basidiomata becoming moveable with age.

Macrochemical tests: positive for tyrosinase throughout basidioma, negative for laccase, negative for KOH and NH_4OH on pileus.

Basidiospores (Fig. 11a) whitish in mass, 9-11(12.5) x 6-7 µm, ($\overline{Q}$ = 1.45), ovoid, broadly ellipsoid to oblong in all views, without germ pore, hyaline in KOH, dextrinoid in Melzer's reagent, metachromatic in Cresyl blue; wall thick, smooth. Basidia (Fig. 11b) clavate, 2-sterigmate, rarely 4-sterigmate, hyaline, inamyloid, 30-35 x (5)8-10 µm. Pleurocystidia absent. Edge of lamellae sterile with abundant cheilocystidia. Cheilocystidia (Fig. 11c) cylindric, sometimes flexuose, rarely septate, often branching at the base, (22)30-52 x 6-8 µm. Hymenophoral trama hyaline, inamyloid, with hyphae 3-8 µm broad, thin-walled, regular to lacunose. Subhymenium pseudoparenchymatous, hyaline, 10-15 µm thick; with cells 5-8(10) µm diam. Pileus trama hyaline, inamyloid, parallel to slightly interwoven but radially arranged; hyphae

3-8(12) µm broad. Suprapileipellis a trichodermium and slightly gelatinized, consisting of narrowly clavate, clavate to subcapitate hyphae (Fig. 11d); hyphae hyaline, inamyloid, often with colorless content, thin-walled, (45)60-90 x 7-15 µm. Subpileipellis of repent hyphae, radially arranged; hyphae cylindric, septate, branching or not, sometimes with diverticula, 3-8(15) µm broad. Stipitipellis of hyphae parallel and vertically oriented, hyaline to yellowish in KOH, thin-walled, often with small diverticula, 3-10 µm broad; at times covered by hyphae similar to those of the suprapileipellis. Annulus of parallel to interwoven hyphae with vertical orientation; hyphae hyaline, cylindric, 3-9 µm broad. Clamp connections abundant on the stipe.

Material studied: COLOMBIA. DPTO. ANTIOQUIA: Mpio. de Gomez Plata, finca La Rochela, a 5 km de Puente Gavito, sobre pasto, 1 May 1991, Franco-M. 575 (HUA, NY); Mpio. Tamésis, vereda Nudillales, jardín de la escuela, sobre pasto, 18 May 1991, Franco-M. 674 (COL, NY). USA. ALABAMA: Auburn, on sandy soil, 2 Sep 1899, E. S. Earle s.n. (HOLOTYPE of Lepiota hortensis Murrill, NY); Same locality, 8 Aug 1898, E. S. Earle s.n. (NY).

Distribution: Known from Alabama, Lesser Antilles (Pegler, 1983), and Colombia.

Discussion: This species seems to be very common on pastures. Despite the presence of clamp connections this species does not belong in Macrolepiota because its basidiospores lack a germ pore. Pegler (1983) considered the presence of 2-sterigmate basidia an interesting feature for the material from Martinique and pointed out that it has not been possible to confirm bisporic basidia in Murrill's holotype. However, after rehydrating in KOH a small fragment of lamella taken from the holotype, I was able to observe basidia which are mostly 2-sterigmate and rarely 4-sterigmate. In addition, the suprapileipellis of the holotype is somewhat gelatinized, and clamp connections are also present and more abundant on the stipe. A germ pore for the species as described by Dennis (1952) was not observed in the examined collections. Although, I have not seen the type of Leucoagaricus bisporus Heinem., its description, as stated by Pegler (1983), is very close to the description of L. hortensis. They may be synonymous.

Leucoagaricus rubrotinctus (Peck) Singer, Sydowia 2: 36. 1948.

FIGS. 12, 13a-d.

≡ <u>Agaricus</u> <u>rubrotinctus</u> Peck, Annual Rep. New York State Mus. 35: 155-156. 1884.

≡ <u>Lepiota</u> <u>rubrotincta</u> Peck, Annual Rep. New York State Mus. 44: 179. 1892.

= <u>Mastocephalus</u> <u>carneoannulatus</u> Clem. Bot. Survey Neb. 4: 17. 1896.

= <u>Lepiota</u> <u>rubriceps</u> Murrill, Bull. Torrey Bot. Club 66: 153. 1939.

Pileus 2-3.5 cm diam, plane with low umbo; surface reddish brown (8F7) at the center, pale brownish red (8C4-8C5) toward the margin, entire, radially splitting or breaking into small granulose scales showing a white context; margin entire to appendiculate, inrolled to decurved. Context ±2 mm thick, white, unchanging. Odor foetid, taste not recorded. Lamellae free, close, ±4 mm broad, white, unchanging; margin entire, not marginate. Stipe up to 6 cm long, 2 mm diam, central, slightly bulbous; surface dry, glabrous, yellowish (2A2) to white, annulate. Annulus membranous, ascendent, white with brownish red (8C4) edge, attached at the center or to the upper third of the stipe.

Macrochemical tests: positive for tyrosinase throughout basidioma, negative for laccase.

Basidiospores (Fig. 13a) white in deposit, 6.3-7.2 x 3.6-4.5 µm ($\overline{Q}$ = 1.67), ovoid to amygdaliform with acute apex in face view, ellipsoid to limoniform in profile, without germ pore, hyaline in KOH, dextrinoid in Melzer's reagent, metachromatic in Cresyl blue. Basidia (Fig. 13b) short clavate to subpyriform, 4-sterigmate, hyaline, inamyloid, 15-18 x 6.3-7.2 µm. Pleurocystidia absent. Edge of lamellae sterile with abundant cheilocystidia. Cheilocystidia (Fig. 13c) cylindric, narrowly clavate to clavate, rarely incrustated, (22)35-55 x 6-10 µm; incrustations dissolving in KOH. Hymenophoral trama hyaline, inamyloid, with hyphae 4-10(20) µm broad, thin-walled, regular to interwoven; subhymenium parenchymatous, ±10 µm wide. Pileus trama hyaline, inamyloid composed of parallel to interwoven but radially oriented hypahe; hyphae cylindric with broadly clavate terminal cells, up to 12 µm broad. Pileipellis (Fig. 13d) a disrupted layer of repent to semierect, parallel to slightly interwoven, radially oriented cylindric hyphae; hyphae hyaline, yellowish or reddish brown in KOH, slightly incrusted, diverticulate or not, often branched, with cylindric to clavate terminal cells with rounded ends, up to 15 µm broad. Stipitipellis of hyphae parallel and vertically oriented, 2-13 µm broad. Annulus of parallel to interwoven and vertically oriented hyphae, hyaline in KOH except at the edge of the annulus where the hyphae are hyaline or reddish brown, sometimes slightly incrusted, 2.5-12 μm broad. Clamp connections absent.

Material studied: COLOMBIA. DPTO. ANTIOQUIA: Mpio. de Medellín, corregimiento de San Cristóbal, vereda San José de La Montaña, bosque mixto con algunos Quercus, 2460 m, 25 Apr 1991, Franco-M. 551 (COL, NY); DPTO. CAUCA: Mpio. de Tunía, vereda El Mango, km 93 de la carretera Cali - Popayán, Reserva Forestal El Guayabo. 2°41′ N 76°32′ W, bosque mixto con Quercus humboldtii, 1640 m, 17 May 1987, G. Mueller 2870 (F); DPTO. QUINDIO: Mpio. de Salento, estación La Montaña, Alto Quindio, sobre hojarasca en bosque de aliso, 2900 m, 26 Apr 1991, A. Peñuela and R. Bernal 428 (COL). USA. FLORIDA: Alachua Co., Gainesville, R. Singer, F2468 (F); NEW YORK: Knowersville and East Worcester, Helderberg Mts, July-september, C. H. Peck s.n. (HOLOTYPE of Agaricus rubrotinctus, NYS).

Distribution: Cosmopolitan. According to Guzmán and Guzmán-D. (1992) the species has been reported from Africa, the Antilles, Asia, Brazil, Canada, Europe, Mexico, and the USA.

Discussion: This is a very handsome mushroom that seems to be easy to identify because of its macroscopic appearance. However, the examination of several American collections determined as Lepiota rubrotincta, not included in this work, shows differences in the size of the basidiospores, size and shape of cheilocystidia, and size and shape of the hyphae forming the pileal and hymenophoral trama that might deserve varietal status. The slightly incrusted cheilocystidia in Franco-M. 551 were not observed in the type but they were reported by Sundberg (1967) from material collected in California.

Lepiota glabridisca Smith and Sundberg differs from Leucoagaricus rubrotinctus in its smaller size and more fragile nature. Furthermore, the pileipellis of Lepiota glabridisca was described by Smith and Sundberg (1979) as two layered and interwoven. Lepiota rubrotinctoides Murrill was thought to be conspecific with L. rubrotinctus by Smith (1954) but differs in having bigger basidiospores, longer cheilocystidia and in the structure of the pileipellis which lacks the broadly clavate terminal cells present in L. rubrotinctus (Fig. 13d).

Lepiota glabridisca and Lepiota rubrotinctoides will be transferred to Leucoagaricus.

Leucoagaricus incrustatus Franco-Molano sp. nov.

Leucoagaricum rubrotinctum (Peck) Singer quammodo simulans, sed basidiomatibus minoribus, basidiosporis minoribus, et cystidiorum distributione necnon forma dissimilis, ulterius cheilocystidiis et pleurocytidiis crassis apice incrustatis notabilis.

Etymology: This species is characterized by having apically incrusted cheilocystidia and pleurocystidia.

FIGS. 14a-d.

Pileus 1.5-2 cm diam, umbonate when young to plane with a low umbo with age; surface dry, glabrous, greyish orange (6B6) at the center, orange (6A5) toward the margin when young, paler (6B7) with age; margin not striate or pectinate, entire to slightly appendiculate with lens. Context thin (±1.2 mm), white, unchanging when bruised or cut. Odor spermatic, taste none. Lamellae free, close, narrow (±2 mm); margin entire to finely serrulate, not marginate. Stipe 4-5 cm long, 2-3 mm broad at the apex, central, equal; surface dry, glabrous, finely fibrillose with lens, white at the apex, yellowish (5B3) or paler toward the base, annulate. Annulus superior, ascendent, membranous, yellowish (5B3), evanescent.

Macrochemical tests: not performed.

Basidiospores (Fig. 14a) whitish in mass, (4.5)5.4-6.3 x 2.7-3.6 µm ($\overline{Q}$ = 1.76), ovoid to amygdaliform in face view, ellipsoid to amygdaliform with acute apex in profile, without germ pore, hyaline in KOH, strongly dextrinoid in Melzer's reagent, slightly metachromatic in Cresyl blue; spore wall thin, smooth. Basidia (Fig. 14b) short clavate to subpyriform, 4-sterigmate, hyaline, inamyloid, 11.7-14.4 x ±6.3 µm. Pleurocystidia (Fig. 14c-d) abundant, ventricose, apically incrusted, thick-walled, hyaline, inamyloid, 35-50 x 8-15 µm. Edge of lamellae sterile with crowded cheilocystidia. Cheilocystidia (Fig. 14c-d) abundant, ventricose, apically incrusted, thick-walled, hyaline with yellowish wall in KOH, inamyloid in Melzer's reagent, 35-50 x 8-15 µm; incrustations soluble in KOH. Hymenophoral trama hyaline, inamyloid, subregular to pseudoparenchymatous, with cylindric to inflated hyphae; hyphae up to ±12 µm broad. Subhymenium pseudoparenchymatous, ±10 µm thick. Pileus trama hyaline, inamyloid, formed of parallel to loosely interwoven but radially oriented hyphae; hyphae cylindric, thin-walled, 2.7-12 µm broad. Pileipellis repent to semierect, formed of hyphae parallel to interwoven with radial orientation, often branched, yellowish in H_2O, hyaline to yellowish in KOH, inamyloid in Melzer's reagent, thin-walled, smooth, 2-12 µm broad. Stipitipellis formed of hyphae parallel and vertically oriented, thin-walled, smooth, 1.8-13.5 µm broad. Annulus tissue of interwoven, cylindric hyphae, often branched, smooth, thin-walled, 2-7 µm broad. Clamp connections absent.

Material studied: COLOMBIA. DPTO. ANTIOQUIA: Mpio. Caldas, vereda La Corrala, ± 25 km S de Medellín, por la variante de Caldas, bosque de *Cupressus*, 1800 m, 5 May 1991, Franco-M. 588 (HUA); DPTO. VALLE, Mpio. de Zarzal, finca El Medio entre el Zarzal y Paila, 940-950 m, 8 Nov. 1988, Franco-M. 124 (HOLOTYPE, CUVC; ISOTYPE, NY).

Distribution: This species is probably neotropical and has been collected only in Antioquia and Valle, Colombia.

Discussion: This small species resembles *Leucoagaricus rubrotinctus* from which it differs by having smaller basidiomata, smaller basidiospores, and in the distribution and shape of the cystidia. This species is characterized by having thick-walled, apically incrusted cheilocystidia and pleurocystidia. It represents an undescribed species which belongs in *Leucoagaricus* due to the absence of a germ pore and the lack of striation on the margin of the pileus.

Leucoagaricus zarzalensis Franco-Molano *sp. nov.*

Leucoagarico americano (Peck) Singer, Lepiota tinctoriae Murrill et L. jamaicensi Murrill arctissime affinis, sed ab iis basidiosporis minoribus poroque germinali nullo diversa.

Etymology: Named for the Municipio de Zarzal, Valle, Colombia.

FIGS. 15, 16a-d.

Pileus 2-7.5 cm diam, convex to plane; surface dry, reddish brown (8E8) overall when young to reddish brown at the center and paler (8E4, 8D4, 8E5) toward the margin when mature, becoming darker to almost black when bruised, finely felty to pubescent, splitting into small squamules; squamules more concentrated at the center and dispersed toward the margin showing a white background; margin crisped, inrolled, short striate. Context up to 4 mm thick, unchanging when cut. Lamellae free, separate from the stipe by a well developed collarium, close to crowded, ±7 mm broad, white becoming red (10B3) when bruised and on drying; margin finely serrate, with marginate edge concolorous with the pileus surface, becoming red (9B6) then dark green-gray (±27E3) when bruised. Stipe up to 7 cm long, 0.8 cm wide, central, equal to bulbous; surface covered whit numerous felty to granulose squamules concolorous with the pileus surface on white to yellowish background, annulate. White rizomorphs at the base. Annulus superior, membranous, fixed at first and becoming moveable with age, white in its inside surface and dark brown (7F8) in its outside surface.

Macrochemical tests: positive for tyrosinase throughout basidioma; positive for laccase throughout basidioma; KOH dark brown on pileus, negative on stipe and lamellae; NH_4OH greyish-green (25C2) on pileus, context, lamellae and stipe.

Basidiospores (Fig. 16a) pure white in mass, 6-8 x 4-5 µm ($\overline{Q}$ = 1.46), broadly ellipsoid to ovoid in all views, without germ pore, hyaline in KOH, dextrinoid in Melzer's reagent, metachromatic in Cresyl blue; wall thin, smooth. Basidia (Fig. 16b) clavate 4-sterigmate, rarely 1- or 2-sterigmate, hyaline, inamyloid, 24-30 x 7-8 µm. Pleurocystidia absent. Edge of lamellae sterile with abundant cheilocystidia. Cheilocystidia (Fig. 16c) utriform, clavate, lanceolate to lageniform, with a flexuose apical prolongation, hyaline or with a dense brown content in H_2O and KOH, inamyloid, 50-100 x 8-12 µm; apical prolongation up to 40 x 5 µm. Hymenophoral trama hyaline, inamyloid, with hyphae 4-10 µm broad, thin-walled, regular to lacunose. Subhymenium pseudoparenchymatous, hyaline, ±15 µm thick; with cells 5-12 µm diam. Pileus trama hyaline, inamyloid, interwoven but radially arranged, hyphae 8-15 (20) µm broad. Pileipellis a trichodermium formed of unicellular hairs (pileocystidiod elements) (Fig. 16d), clavate, broadly clavate, ventricose to fusoid, often with apical prolongation, filled with yellowish brown to dark content in KOH, greyish green in NH_4OH, rather thick-walled, 50-140(200) x 10-22 µm; apical elongation up to 50 x ±5 µm. Stipitipellis composed of interwoven unicellular hairs similar to those forming the pileipellis. Annulus tissue formed in its inner side by parallel but radially oriented hyphae giving rise to tufts of cystidioid elements similar to those forming the pileipellis; in its outer side similar to stipitipellis. Clamp connection absent.

Material studied: COLOMBIA. DPTO. VALLE: Mpio. de Zarzal, Finca El Medio, entre El Zarzal y Paila, sobre pasto bajo una Ceiba, 940-950 m, 4 May 1990, Franco-M. 409 (HOLOTYPE, COL; ISOTYPES, CUVC, NY).

Distribution: It has been collected only in Dpto. del Valle, Colombia.

This is an undescribed species very closely related to Leucoagaricus americanus (Peck) Singer, Lepiota tinctoria Murrill, and Lepiota jamaicenses Murrill from which it differs in having smaller basidiospores and lacking a germ pore. Because of the lack of a germ pore in the basidiospores, the color change when bruised, the green reaction to NH_4OH, and the cystidioid elements forming the pileipellis, this species also resembles Leucoagaricus georginae (W. H. Smith) Candusso and L. badhamii (Berk. and Br.) Singer, but it does not stain bright red when bruised and lacks the two layered pileipellis of L. georginae. In L. badhamii the pileipellis is formed of elongate, unicellular hairs, with tapered apex and rounded tips and the stipitipellis lacks differentiated hairs while in Leucoagaricus zarzalensis both pileipellis and stipitipellis are formed by unicellular hairs (cystidioid elements), that are clavate, broadly clavate, ventricose to fusoid, often with apical prolongation, and filled with yellowish brown to dark content. In addition, L. badhamii seems to be a temperate species growing under yew and L. zarzalensis is a tropical species collected under Ceiba sp. It belongs in Singer's section Pilosellae.

Leucoagaricus guachacanus Franco-Molano sp. nov.

Pileipelli repenti, basidiosporis destrinoides metachromaticis, basidiosporisque delicatim ornatis et minutim porosis praestans, L. pulverulento proxima sed basidiosporis majoribus necnon cheilocystidiis diversa.

Etymology: Named for the Municipio de Guachaca, Magdalena, Colombia.

FIGS. 17a-d, 18.

Pileus 3 cm diam, plane; surface dry, finely squamulose; squamules more concentrated at the center and dispersed toward the margin, pale brown (6C6) on white background. Context up to 2 mm thick, white, unchanging when exposed. Lamellae free, close, 3 mm broad; margin entire, not marginate. Stipe 5 cm long, 2 mm wide, equal to subbulbous; surface finely squamulose to tomentose, pale brown (6C5) overall, annulate. Annulus superior, membranous, descendant, evanescent.

Macrochemical reactions: not performed.

Basidiospores (Fig. 17a) white in mass, 6-8 x 3-4 µm ($\bar{Q}$ = 1.69), ellipsoid to oblong often with median constriction in face view, ellipsoid, oblong to subcylindrical, often constricted at the middle in profile, with a tiny germ pore, hyaline in KOH, dextrinoid in Melzer's reagent, metachromatic in Cresyl blue; spore wall thin, finely verrucose ornamented (Fig. 18). Basidia (Fig. 17b) short clavate, 4-sterigmate, hyaline, inamyloid 16-20 x 6-7 μm. Pleurocystidia absent. Edge of lamellae sterile with crowded cheilocystidia. Cheilocystidia (Fig. 17c) broadly clavate, clavate, cylindric to flexuose, at times with a short mucronate apex, 25-40 x 5-8 μm. Hymenophoral trama hyaline, inamyloid, regular, with hyphae 3-6 μm. Subhymenium pseudoparenchymatous, hyaline, ±10 μm thick; with cells 5-10 μm broad. Pileus trama hyaline, inamyloid, parallel with radial orientation, with hyphae 2-7 μm broad. Pileipellis (Fig. 17d) formed of repent to semierect interwoven hyphae; hyphae cylindric, hyaline to yellowish in KOH, branched or not, with narrowly clavate terminal cells, 7-10(12) μm broad. Stipitipelis formed of the same kind of tissue forming the pileipellis. Annulus formed of two kinds of tissues: the inner side possesses formed of parallel and vertically oriented hyphae, hyaline to yellowish in KOH, 2-4 μm broad; the outer side is formed of interwoven hyphae similar to those forming the pileipellis, yellowish in KOH, 5-10 μm broad. Clamp connections absent.

<u>Material studied</u>: COLOMBIA. DPTO. MAGDALENA: Mpio. de Guachaca, Sierra Nevada de Santa Marta, camino a Ciudad Perdida entre Machete y Buenavista, 1480 m, 14 Jun 1992, <u>Franco-M. 961</u> (HOLOTYPE, COL).

Distribution: Known only from Sierra Nevada de Santa Marta, Colombia.

Discussion: This undescribed species is characterized by having a repent pileipellis, dextrinoid, metachromatic, and finely ornamented basidiospores (Fig. 18) with a tiny germ pore. Although, *Leucoagaricus pulverulentus* has been described as having slightly ornamented basidiospores (Candusso and Lanzoni, 1990; Migliozzi *et al.*, 1989) it differs from *L. guachacanus* in having smaller basidiospores and lacking cheilocystidia. In addition, the pileipellis of *L. pulverulentus* is formed of ±catenulate hyphae while *L. guachacanus* is formed of cylindric hyphae with well defined terminal cells.

Singer (1972) created the section *Sculpturati* of *Leucoagaricus* to accommodate *L. rubrosquamosus* (Rick) Sing. [= *Rugosospora pseudorubiginosa* (Cifuentes and Guzmán) Guzmán and Bandala] that together with *Leucoagaricus pulverulentus* are the only known species with ornamented basidiospores in the tribe. However, *L. guachacanus* differs from *R. pseudorubiginosa* in the lack of a hymeniform pileipellis and clamp connections, and in the ornamentation of the basidiospores. The basidiospores of *R. pseudorubiginosa* are rugulose to reticulate while in *Leucoagaricus guachacanus* the basidiospores are finely verrucose. Thus, I refer L. guachacanus to Leucoagaricus section Sculpturati.

Leucocoprinus Patouillard

Bull. Soc. Mycol. France 4: 26. 1888.

Hiatula (Fr.) Mont. emend. Heim & Romagn., Bull. Soc. Mycol. France 50: 186. 1934

Lepiota subg. Leucobolbitius J. Lange, Fl. Agar. Danica 1: 20. 1935.

Lepiota sect. Striatae Murrill, N. Amer. Fl. 10: 42. 1914.

Lepiota sect. Cepaestipedes Konr. and Maubl., Icon. Select. Fung. 6: 41. 1937.

Type species: Lepiota cepaestipes (Sow.:Fr.) Kummer [Leucocoprinus cepaestipes (Sow.:Fr.) Pat.]

The genus was created by Patouillard (1888) to include the species of Lepiota whose basidiospores possess a germ pore. Macroscopically, the genus is characterized by having small to medium, often fragile basidiomata with lepiotoid to coprinoid habit. Pileus thin, membranous; surface floccose, squamulose to fibrillose scaly, striate at least at the margin. Context thin, staining or not upon bruising. Lamellae free, thin, crowded, sometimes deliquescent. Stipe central, equal to bulbous. Annulus membranous, evanescent. Spore print white. Microscopically, the basidiospores are characterized by having a broad germ pore, but sometimes the germ pore is not distinctive, metachromatic endosporium, and a smooth, simple to complex spore wall. The hymenophoral trama is regular to lacunose. The pileipellis is variable throughout the species; it can be an epithelium formed of different kinds of cells, a trichodermium or a hymeniform layer and occasionally sphaerocysts are present. Pleurocystidia are sometimes present. Cheilocystidia are abundant. Clamp connections are absent.

Although Singer (1986) differentiated Leucoagaricus from Leucocoprinus by the long pectinate pileus, especially when mature in the latter, and the thick, more fleshy pileus in Leucoagaricus, these features by themselves have little taxonomic value. A pectinate or striate pileus surface is found in species with a fleshy pileus like Leucoagaricus americanus (Peck) Singer, L. badhamii (Berk. and Br.) Singer and related species [= Leucocoprinus badhamii complex (Reid, 1990)], and a rather thin pileus with entire surface is found in Leucocoprinus sulphurellus Pegler. In distinguishing the above genera, pseudoparaphyses (brachycystidia or pavement cells) and polymorphic basidia which are well-developed in Leucocoprinus (Singer, 1986) can also be diagnostic. However, paraphyses may occur in Leucoagaricus and in Lepiota s.s.

In addition, the observation of these characters are not always possible, depending on how well the lamellae revive and on how thin the cross sections of lamellae are made. Paraphyses and/or polymorphic basidia are by themselves of little taxonomic importance; they should be combined with other characters for an accurate determination. In this work, all the species of Leucocoprinus included are characterized by the combination of thin pileus and the presence of pseudoparaphyses. Well differentiated polymorphic basidia were observed in two species, L. fragilissimus and L. cepaestipes.

Key to species found in Colombia

1. Pileus surface white, whitish or yellow.

    2. Pileus surface white when young, becoming greyish-brown or greyish yellow with age, not staining when bruised; stipe subbulbous to bulbous; pleurocystidia absent; cheilocystidia clavate to ventricose, often mucronate, 30-80 x 10-16 µm; mucronate apex flexuose, often constricted, sometimes branched abundant.. L. cepaestipes, p. 131

2. Pileus surface yellow, staining or not when bruised; stipe equal; spite equal; pleurocystidia present or not; cheilocystidia of various shapes, 7-13 x 4-10 μm, abundant.

    3. Pileus surface bright yellow, entire at the center, floccose squamulose toward the margin; plicate striate except at the center; context white, unchanging when bruised; basidiospores 11-13 x 8-10 μm; pleurocystidia absent; cheilocystidia pyriform.......................
    L. fragilissimus, p. 134

    3. Pileus surface greyish yellow, entire at the center, fibrillose to fibrillose scaly toward the margin on sulphur yellow background; context yellow becoming blue when bruised; basidiospores 7-8 x 4-5 μm; pleurocystidia fusoid, ventricose to mucronate; cheilocystidia fusoid, ventricose to mucronate
    L. sulphurellus, p. 125

1. Pileus surface red-brown, brown or possessing brown scales on whitish background.

4. Pileus surface red brown, breaking into granulose squamules on white background; basidiospores 6-7 x 4-5 µm, ellipsoid to ovoid, rounded at the apex; suprapileipellis two layered formed of a hymeniform base given rise to a trichodermium of clavate to fusoid, often mucronate elements; pleurocystidia pyriform... *L. zamurensis*, p. 122

4. Pileus surface greyish brown, breaking into fine squamules toward the margin on greyish background; basidiospores 8-10 x 6-7 µm ovoid to amygdaliform with acute apex; pileipellis one layered, hymeniform; pleurocystidia absent.................. *L. tenellus*, p. 128

Leucocoprinus zamurensis (Pat. & Gaill.) Franco-Molano, *comb. nov.*

FIGS. 19a-e.

≡ *Lepiota zamurensis* Pat. & Gaill. sensu Dennis, Kew Bull. 7: 482. 1952.

Pileus 4-5 cm diam, convex to plane with low umbo; surface dry, plicate-striate, brown (7E7) to reddish brown

(9E7), breaking into finely granulose squamules more concentric at the center, on white background. Context 2 mm thick, white, unchanging. Odor none, taste not recorded. Lamellae, free, close, thin, ±3 mm broad, white, staining reddish brown when bruised; margin entire, not marginate. Stipe 3-7.5 cm long, 3 mm wide near the apex, central, subbulbous; surface finely granulose, brown (6C4) or paler, annulate. Annulus superior, membranous, concolorous with the stipe, evanescent.

Macrochemical tests: positive for tyrosinase throughout basidioma; positive for laccase throughout basidioma; KOH on pileus, yellowish; NH_4OH on pileus, dark grey then reddish.

Basidiospores (Fig.19a) white in mass, 6-7 x 4-5 μm ($\overline{Q}$ = 1.53), broadly ellipsoid to ovoid in all views, without germ pore, hyaline in KOH, dextrinoid in Melzer's reagent, metachromatic in Cresyl blue; spore wall thin, smooth. Basidia (Fig. 19b) short clavate to broadly clavate, 4-sterigmate, hyaline, inamyloid, ±16 x 10 μm. Pseudoparaphyses well differentiated, ovoid, hyaline in KOH, 11-16 x 7-12 μm. Pleurocystidia (Fig. 19d) globose to sphaeropedunculate, hyaline or with brown content in KOH, inamyloid, thin-walled, 45-55 x 23-30 μm. Edge of lamellae sterile with crowded cheilocystidia. Cheilocystidia

(Fig. 19c) oblong, utriform, obpyriform to clavate, sometimes mucronate, hyaline or with brown content in KOH, 45-62 x 15-18 µm. Hymenophoral trama hyaline, inamyloid, with hyphae up to 10 µm broad, regular to lacunose. Subhymenium pseudoparenchymatous, up to 15 µm thick, with cells 5-7 µm wide. Pileus trama hyaline, inamyloid, with hyphae 4-8 µm broad, thin-walled, slightly interwoven but with radial orientation. Suprapileipellis (Fig. 19e) two layered, with hymeniform basal layer, composed of clavate, broadly clavate to sphaeropedunculate hyphae, 40-65 x 20-30 µm, hyaline or with brown content in KOH, from which a disrupted trichodermal palisade of erect, elongate, clavate to fusoid, often mucronate, elements arise; elements brown in KOH, thin-walled, 80-130 x 15-20 µm. Subpellis of pileus repent, formed of parallel to interwoven hyphae with radial orientation; hyphae hyaline to yellowish brown in KOH, often incrusted, up to 10 µm broad. Stipitipellis formed of parallel, vertically oriented hyphae; hyphae 2-15 µm broad, with cystidioid terminal cells; terminal cells clavate to fusoid, often mucronate, 50-70 x 12-15 µm. Annulus tissue reviving poorly in KOH, but cystidioid elements similar to those on suprapileipellis present. Clamp connections absent.

<u>Material</u> <u>studied</u>: COLOMBIA. DPTO. META: Mpio. de Puerto Gaitan, Centro de Investigaciones ICA-CIAT,

Carimagua, motobomba Yapuré, 19 May 1992, Franco-M. 857 (COL, NY). MARTINIQUE: Precheur, Anse Couleuve, on forest floor, 20 Sep 1977, Pegler 2802 (K); Trinité, 2 Oct 1977, Pegler 2940 (K). TRINIDAD: Arena forest, 30 Sep 1949, Dennis 251 (K); Siparia Forest Bungalow, 5 Nov 1949, Dennis 251A (K).

Distribution: Neotropical, Lesser Antilles and Colombia.

Discussion: Lepiota zamurensis was described by Patouillard and Gaillard (1888) from Puerto Zamuro, Venezuela, but the type has not been located. Thus, my concept follows that of Pegler (1983). Although pleurocystidia were not observed by Dennis or Pegler, all examined collections had clavate, subglobose to sphaeropedunculate pleurocystidia with a very thin wall. The transfer of this species to Leucocoprinus is based on the metachromasy of the basidiospores, the paraphyses of the hymenium, and the fragility of the pileus.

Leucocoprinus sulphurellus Pegler, Kew Bull. Add. Ser. 9: 420. 1983.

FIGS. 20, 21a-e.

Pileus 1-3 cm broad, convex to plano-convex with a small umbo; surface dry, greyish yellow (4C4) to light brown (6D6), entire at the center, fibrillose to fibrillose scaly toward the margin on yellow (2A3-2A4) background; margin appendiculate, entire. Context ±1 mm thick, yellow (2A3-2A4), staining blue when exposed. Lamellae free, close, up to 3 mm broad, yellow (1A4, 2A3, 2A4), staining blue then black when bruised; margin entire, not marginate. Stipe 2-3.5 cm long, up to 1.5 mm wide, central, equal; surface smooth and glabrous to finely fibrillose with lens, concolorous with lamelllae, staining blue then black when bruised, annulate. Annulus superior, thin, membranous, concolorous with pileus surface, fugacious. Yellowish mycelium at the base.

Macrochemical test: not performed.

Basidiospores (Fig. 21a) white in mass, basidiospores 7-8(9) x 4-5 μm ($\overline{Q}$ = 1.83), ellipsoid to oblong, with truncate apex in all lateral views, hyaline in KOH, dextrinoid in Melzer's reagent, metachromatic in Cresyl blue, smooth, rather thick-walled, with small germ pore. Basidia (Fig. 21b) broadly clavate, 4-sterigmate, hyaline, inamyloid, 20-22 x 8-10 μm. Pseudoparaphyses subglobose, hyaline, ±15 x 10 μm. Pleurocystidia (Fig. 21d) fusoid, ventricose, mucronate, 30-45 x 10-12 μm. Edge of lamellae with abundant cheilocystidia. Cheilocystidia (Fig. 21c) fusoid, ventricose, mucronate, 50-70 x 10-12 µm; mucronate apex flexuouse, often capitate, 7-15 x 2-5 µm. Hymenophoral trama hyaline, inamyloid, regular, with hyphae 5-12 µm broad, thin-walled. Subhymenium pseudoparenchymatous, up to 15 µm thick, with cells 6-12 µm wide. Pileus trama hyaline to yellow in KOH, inamyloid, formed of parallel, radially arranged hyphae; hyphae 5-15 µm broad. Pileipellis (Fig. 21e) epithelial, formed of cylindric to catenulate, loosely interwoven hyphae with cylindric, clavate, globose to ovoid cells, hyaline to yellowish or with yellowish brown content, up to 22 µm broad. Stipitipellis of hyphae parallel and vertically oriented, yellowish in KOH, thin-walled, 3-15 µm broad. Annulus tissue not recovered. Clamp connections absent.

Material studied: COLOMBIA. DPTO. ANTIOQUA: Mpio. de Caldas, vereda La Corrala, ±25 km S de Medellín por la variante a Caldas, bosque de Cupressus, 1800 m, 4 May 1991, Franco-M. 583 (HUA, NY); 5 May 1991, Franco-M. 583 (COL, HUA, NY); Mpio. de Jardin, vereda El Cuchillón, a orillas de la Quebrada, bosque mixto a 2000 m, 9 Jun 1991, Franco-M. 732 (NY). COSTA RICA. PROV. PUNTARENAS: Finca Las Alturas, NW boundary with buffer zone of Parque La Amistad, forest of Quercus pilarius, 1500-1600 m, 7 Nov 1989, Franco-M. 301 (NY); Zona Protectora Las Tablas, Parque La Amistad, bosque de *Quercus pilarius*, *Alchornea sp.*, *Saccoglotis sp.*, *Ulmus mexicanus*, 1500-1750 m, 11 Nov 1989, *Franco-M. 323* (NY). MARTINIQUE: Regale, in banana plantation, 2000 m, 5 Aug. 1975, *Fiard 175* (HOLOTYPE, K); Precheur, Hauter Anse Couleuvre, on Forest soil, 20 Sep 1977, *Pegler 2815* (PARATYPE, K); 23 Sep 1977, *Fiard 992* (PARATYPE, K). GUADALOUPE: Basse Terre, Ste-Rose, Trace de Sofaia, solitary in mesophytic forest, 25 Oct 1977, *Pegler 3125* (PARATYPE, K).

Distribution: Neotropical.

Discussion: This species is very easy to recognize by the yellow color of the basidiomata that stain bright blue then black when bruised. Even though it has a non-striate pileus margin, Pegler placed it in *Leucocoprinus* because of its pleurocystidia, the cheilocystidia shape and the complex structure of the basidiospores with a germ pore. The epithelial pileipellis and the presence of pseudoparaphyses are also typical of *Leucocoprinus*.

Leucocoprinus tenellus Pegler, Kew Bull. Add. Ser. 9: 425. 1983.

FIGS. 22a-c.

Pileus 0.6-2 cm diam, campanulate to plane; surface dry, pale greyish brown (8E3), entire at the center, splitting into fine squamules toward the margin on greyish background, plicate from margin to center. Context thin (less than 1 mm thick at the disk), grayish brown. Lamellae free, close, very thin, up to 5 mm broad, whitish, unchanging when bruised. Stipe 2-7 cm long, 2 mm wide near the apex, central, equal to subbulbous, smooth to finely fibrillose, whitish to reddish gray (7B2), annulate. Annulus superior but near the middle of the stipe, membranous, white.

Macrochemical tests: positive for tyrosinase throughout basidioma; negative for laccase.

Basidiospores (Fig. 22b) white in mass, (7)8-10 x 6-7(9) μm ($\bar{Q} = 1.34$), ovoid to amygdaliform with apex truncated by a broad germ pore, hyaline in KOH, dextrinoid in Melzer's reagent, metachromatic in Cresyl blue; spore wall thick and complex, smooth. Basidia (Fig. 22c) broadly clavate to pyriform, 4-sterigmate, hyaline, inamyloid, 20-26 x 10-13 μm. Pleurocystidia absent. Edge of lamellae not recovered. Cheilocystidia probably absent. Hymenophoral trama regular at first then lacunose, hyaline, inamyloid; hyphae cylindric, branched or not, 4-10 μm broad, with broadly clavate to pyriform terminal cells forming the hymenium. Subhymenium not differentiated. Pileus trama hyaline, inamyloid, interwoven but radially arranged, hyphae 4-12(17) μm broad. Pileipellis (Fig. 22a) hymeniform, formed of catenulate hyphae; hyphae formed of globose, broadly clavate to pyriform cells, hyaline to brownish in KOH, rarely incrusted, thin-walled, 17-45 x 10-15 μm. Stipitipellis of hyphae parallel and vertically oriented, hyaline, thin-walled, 4-18 μm broad. Annulus formed of densely interwoven cylindric hyphae; hyphae hyaline in KOH, thin-walled, 2-9 μm broad. Clamp connections absent.

Material studied: COLOMBIA. DPTO. META: Mpio. de Puerto Gaitan, Centro de Investigaciones ICA-CIAT, Carimagua, Ensayo Caribey, 12 May 1992, Franco-M. 872 (COL, NY). MARTINIQUE: Vallée de la Riv. Lorrain, on soil in banana plantation, 30 Sep 1977, Pegler 2893 (HOLOTYPE, K).

Distribution. Neotropics (Peger, 1983), including Colombia and Martinique

Leucocoprinus tenellus is a very fragile species closely related to *L. fragilissimus* from which it differs in the color of the basidiomata which is greyish brown in the former and bright yellow in the later.

Leucocoprinus cepaestipes (Sow.:Fr.) Pat., Tab. Analyt. Fung. Fasc. 7:45. 1889.

FIGS. 23, 24a-e.

≡ Agaricus cepaestipes Sow.:Fr., Syst. Mycol. 1: 280. 1821.

≡ Lepiota cepaestipes (Sow.:Fr.) Kummer, Führ. Pilzk.: 136. 1871.

≡ Mastocephalus cepaestipes (Sow.:Fr.) Kuntze, Rev. Gen. Pl. 2: 859. 1891.

≡ Hiatula cepaestipes (Sow.:Fr.) Heim & Romagn., Bull. Soc. Mycol. France 50: 184. 1934.

= Agaricus continuus Berk. in Hook., Lond. J. Bot. 6: 480. 1847.

≡ Lepiota continua (Berk. & Br.) Sacc., Syll. Fung. 5: 44. 1887.

= Agaricus rorulentus Panizzi, Comm. Soc. Critt. Ital. 172. 1847.

≡ Lepiota rorulenta (Panizzi) Barla, Bull. Soc. Myco. France 9: 117. 1886.

= Agaricus cheimonoceps Berk. & Curt., J. Linn. Soc. Bot. 10: 283. 1869.

≡ Lepiota cheimonoceps (Berk. & Curt.) Sacc., Syll. Fung. 5: 66. 1887

= Agaricus oncopus Berk. & Br., J. Linn. Soc. Bot. 11: 496. 1871.

≡ Lepiota oncopus (Berk. & Br.) Sacc., Syll. Fung. 5: 44. 1887.

= Agaricus oenopus Berk. & Br., J. Linn. Soc. Bot. 11: 499. 1871.

≡ Lepiota oenopus (Berk. & Br.) Sacc. Syll. Fung. 5: 57. 1887.

= Agaricus adoreus Berk. & Br., J. Linn. Soc. Bot. 11: 499. 1871.

≡ Lepiota adorea (Berk. & Br.) Sacc. Syll. Fung. 5: 44. 1887.

Pileus 2-7 cm diam, ovoid, convex to plano-convex with low umbo; surface dry, white when young, becoming grayish brown (8E3) to greyish yellow (4B3) with age, entire at the center, squamulose toward the margin on white to creamy background; margin entire at first, striate in mature basidiomata. Context up to 1.5 mm thick, white when young, creamy to grayish brown with age. Odor and taste not distinctive. Lamellae free, close, up to 6 mm broad, whitish; margin finely fimbriate. Stipe 2-8 cm long, 1.5-3 mm wide, central, subbulbous to bulbous; surface pruinose, white to grayish brown (8B3), annulate. Annulus superior, flaring, membranous, white to whitish, persistent to evanescent.

Macrochemical test: positive for tyrosinase throughout basidioma; positive for laccase but only at the base of the stipe.

Basidiospores (Fig. 24a) white in mass, 9-11(12) x 6-7 μm ($\overline{Q}$ = 1.58), ovoid with apex truncated by a broad germ pore in all lateral views, hyaline in KOH, dextrinoid in Melzer's reagent, metachromatic in Cresyl blue; spore wall smooth, thick, complex. Basidia (Fig. 24b) narrowly clavate, clavate to broadly clavate, 4-sterigmate, hyaline, inamyloid, 20-35 x 8-12 μm. Pleurocystidia absent. Edge of lamellae with abundant cheilocystidia. Cheilocystidia (Fig. 24c) clavate to ventricose, mostly mucronate, 30-80 x 10-16 μm; mucronate apex flexuose, often constricted, sometimes branched, 10-20 x 4-5 μm. Hymenophoral trama regular to lacunose, with hyphae 2-7 μm broad. Subhymenium pseudoparenchymatous, ±12 μm thick; with cells 4-7 μm wide. Pileus trama hyaline, inamyloid, parallel but radially arranged; hyphae cylindric, often anastomosing, thin-walled, 2-8 μm broad. Pileipellis (Fig. 24d) a trichodermium formed of narrowly clavate, cylindric to flexuose hyphae; hyphae hyaline or with yellowish brown content in KOH, 30-110 x 5-7 μm. Stipitipellis (Fig. 24e) formed of hyphae similar to those forming the pileipellis; hyphae loosely interwoven but vertically oriented, up to 8 μm broad. Annulus tissue of densely interwoven hyphae in its inner side, hyphae up to 12 μm broad; outer side formed of hyphae similar to those forming the pileipellis. Clamp connections absent.

Material studied: COLOMBIA. DPTO. ANTIOQUIA: Mpio. de Medellín, Avenida Nutibara, en un jardín, 6 Jun 1990, Franco-M. 518 (HUA, NY); DPTO. META: Mpio. de Puerto Gaitan, Centro de Investigaciones ICA-CIAT, Carimagua, Ensayo Caribey, 22 May 1993, Franco-M. 851 (COL, NY). GREAT BRITAIN. Surrey: Kew, Royal Botanic Garden, palm house, 18 Sep 1990, Franco-M. 545 (COL, HUA, NY); 18 Sep 1990, Franco-M. 548 (NY). USA. NEW YORK: Bronx Co., New York Botanical Garden, in wood chip mulch,.near hemlock forest, 6 Aug 1986, A. Methven s.n. (NY).

Distribution: Cosmopolitan, common in tropics and subtropics.

Leucocoprinus cepaestipes is a saprophytic species, very common in greenhouses and areas rich in humus. It is very close to the yellow L. birnbaumii (Corda) Singer from which differs in the color of the basidiomata.

Leucocoprinus fragilissimus (Rav.) Pat., Essai Taxon. 171. 1900. FIGS. 25, 26a-e.

≡ Hiatula fragilissima Rav. apud Berk. and Curt., Ann. Mag. Nat. Hist. ser. 2, 12: 422. 1853.

≡ Agaricus fragilissimus (Rav.) P. Henn., Engl. and Prantl, Nat. Pfl.-Fam. 1, 1: 263. 1900.

≡ Lepiota fragilissima (Rav.) Morgan in J. Mycol. 13: 5. 1907.

= Agaricus licmophorus Berk. & Br ., J. Linn. Soc. Bot. 11: 500. 1871.

≡ Lepiota licmophora (Berk. & Br.) Sacc., Syll. Fung. 5: 44. 1871.

≡ Mastocephalus licmophorus (Berk. & Br.) Kuntze, Rev. Gen. Pl. 2: 860. 1891.

≡ Hiatula licmophora (Berk. & Br.) Petch, Ann. Roy. Bot. Gard., Peradineya 4: 385. 1910.

≡ Leucocoprinus licmophorus (Berk. & Br.) Pat., Bull. Soc. Mycol. France 29: 216. 1913.

Pileus 2-4.5 cm diam, campanulate to plane, often slightly depressed at the center; surface entire and bright yellow (3A4-3A5) before the pileus expands, plicate striate to the center, whitish almost translucent with yellow (3A4-3A5) squamules on the radial ridges, and entire at the center when expanded. Context very thin, white. Lamellae, free, close, very thin, up to 2.5 mm broad, white, unchanging when bruised. Stipe 5-10 cm long, ±1.5 mm wide near the apex, equal, greenish yellow with yellow (3A3) floccose squamules, annulate. Annulus superior, ascendent, membranous, yellowish, evanescent.

Macrochemical tests: not performed.

Basidiospores (Fig. 26f) white in mass, 11-13(14) x 8-10 μm($\overline{Q}$ = 1.4), broadly ellipsoid but strongly constricted apically into a short cylindric region terminated by a broad germ pore, hyaline in KOH, dextrinoid in Melzer's reagent, metachromatic in Cresyl blue; spore wall thick and complex, smooth. Basidia (Fig. 26b) pyriform, clavate to broadly clavate, hyaline, inamyloid, 18-32 x 10-12 μm. Pseudoparaphyses (Fig. 26b) subglobose to ovoid, 15-16 x 11-14 μm. Pleurocystidia absent. Edge of lamellae fertile with abundant cheilocystidia. Cheilocystidia (Fig. 26a) broadly clavate to pyriform, hyaline, 16-22 x 12-15 μm. Hymenophoral trama regular at first then lacunose, hyaline, inamyloid, formed of hyphae 3-9 μm broad. Subhymenium pseudoparenchymatous 10-15 μm thick; cells 5-7 μm broad. Pileus trama hyaline, inamyloid, with parallel to radially arranged cylindric hyphae, 2-9 μm broad. Suprapileipellis, (Fig. 26c) in scalp section, an epithelium formed of globose cells, hyaline in KOH, 20-30 μm broad. Subpileipellis (Fig. 26e) formed of parallel to slightly interwoven hyphae, cylindric, often moniliform, branched or not, hyaline to yellow in KOH, 5-10 μm broad.

Stipitipellis of hyphae parallel to vertically oriented, yellowish in KOH, thin-walled, 5-15(25) µm broad. Annulus tissue on its inner side is similar to the tissue forming the subpileipellis and the tissue of its outer side is formed of globose cells similar to the cells forming the suprapileipellis. Clamp connections absent.

Material studied. COLOMBIA. DPTO. META: Mpio. de Puerto Gaitan, Centro de Investigaciones ICA-CIAT, Carimagua, Motobomba Yapure, 19 May 1993, Franco-M. 852. (COL). USA. FLORIDA: Alachua Co., Austin Care Memorial Forest, Mize Lake, 11 Aug 1985, H. E. Bigelow 19100 (NY).

Distribution: Pantropical (Pegler, 1983)

Discussion: The bright yellow color and the fragility of the basidiomata distinguish this species. The basidiomata of this species collapse as soon as it is touched. Thus, notes about its macroscopic features are to be taken before touching it. According to Pegler (1983) this is a common pantropical species which is rarely collected due to its fragility.

Rugosospora Heinemann

Bull. Jard. Bot. Nat. Belg. 43: 12, 1973.

Type species: Lepiota ochraceobadia Beeli

The genus was created by Heinemann (1973b) based on Lepiota ochraceobadia Beeli (1932) and Lepiota lateritia Beeli (1936) from central African material. It includes species having a thin, submembranaceous pileus with pyriform cells forming a hymeniform pileipellis; metachromatic, rugulose basidiospores, and possessing clamp connections.

Key to species

1. Basidiospores rugulose, 8-12(14.5) x 4.4-6(6.8) µm..
R. ochraceobadia (Beeli) Heinemann (extralimital)

1. Basidiospores reticulate, 8-10 x (4)5-6 µm.............
R. pseudorubiginosa, p. 138

Rugosospora pseudorubiginosa (Cifuentes & Guzmán) Guzmán & Bandala, Brenesia 32: 107-112. 1989.

FIGS. 27, 28a-e, 29a-c, 30.

≡ _Lepiota_ _pseudorubiginosa_ Cifuentes & Guzmán, Bol. Soc. Mex. Mic. 16: 48. 1981.

= _Lepiota_ _epicharis_ var. _occidentalis_ Dennis, Kew Bull. 15: 111. 1962. _syn._ _nov._

= _Lepiota_ _rubro-squamosa_ Rick ss Singer, Brotéria Sér. Bot. 18: 50. 1920.

≡ _Leucoagaricus_ _rubrosquamosus_ (Rick) Singer, Lilloa 22: 422. 1949 (1951). _syn._ _nov._

Pileus 1-5 cm diam, convex to plane with low umbo; surface dry, entire at the center, appressed fibrillose-scaly toward the margin; scales brown (7D7) to reddish brown (8D7, 8E7, 8E8, 9E7), on white background; margin appendiculate in young specimens, entire to slightly pectinate with age. Context up to 2 mm thick, white, unchanging when exposed. Odor and taste not distinctive. Lamellae free, close, ±4 mm broad, white, staining brown (6D7) when bruised; margin entire, not marginate. Lamellulae of four lengths. Stipe up to 10 cm long, 2.5-4 mm wide, central, equal to slightly bulbous; surface shiny, fibrillose, white at the apex, pale orange (5A3-4) to brown orange (7C3) at the base or brown orange (7C3) overall, annulate; white mycelium at the base. Annulus superior, ascendent, membranous, concolorous with pileus surface on the outer side, and white to yellowish inside, fixed in young specimens but becoming moveable with age.

Macrochemical tests: positive for tyrosinase throughout basidioma; positive for laccase throughout basidioma; KOH on pileus, grayish; negative for NH_4OH on pileus.

Basidiospores (Fig. 28a) white in mass, 8-10 x (4)5-6 µm ($\overline{Q}$ = 1.7), ellipsoid, oblong to cylindric in face and profile views, hyaline in KOH, dextrinoid in Melzer's reagent, metachromatic in Cresyl blue; ornamentation forming a raised reticulum in mature basidiospores, reaching up to 1.6 µm high. Basidia (Fig. 28c) clavate, broadly clavate to almost pyriform, mostly 2-4-sterigmate, rarely 1-sterigmate, hyaline, inamyloid, (18) 25-35 x (8)9-13 µm. Pleurocystidia absent. Edge of lamellae sterile with abundant cheilocystidia. Cheilocystidia (Fig. 28b) cylindric, clavate to pyriform, rarely septate, 18-40 x 6-11 µm. Hymenophoral trama hyaline, inamyloid, with hyphae 4-12(17) µm broad, thin-walled, parallel to slightly interwoven. Subhymenium pseudoparenchymatous, hyaline, up to 20 µm thick; with cells 5-17 µm wide. Pileus trama hyaline, inamyloid, parallel to slightly interwoven but radially arranged, hyphae of 4-15(22) µm broad. Pileipellis (Fig. 28e) hymeniform, consisting of clavate, pyriform to pedicellate cells; cells yellowish red in H_2O, reddish or yellowish to hyaline in KOH, inamyloid, thin-walled, 20-80 x 10-20 µm. Stipitipellis of hyphae parallel and vertically oriented, hyaline to yellowish in H_2O and KOH, thin-walled, 5-12(20) µm broad. Annulus formed of two different tissues: the inner side is formed of densely interwoven hyphae, hyaline, 2-7 µm broad; the outer side is formed of clavate to pyriform cells, similar to those forming the pileipellis, hyaline to yellowish in H_2O and KOH, 20-50 x 10-16 µm. Clamp connections present.

Material studied of Rugosospora ochraceobadia (all African): CONGO. Orston: Broygandle, Nov. 1967, K. Grinling 71129 (K); Brazzaville, Feb 1965, K. Grinling 50219 (K); Mar 1965, K. Grinling 50324 (K); ZAIRE. Binga, Apr 1928, Goossens-Fontana 666 (HOLOTYPE of Lepiota ochraceobadia, BR); Apr 1928, Goossens-Fontana 665 (HOLOTYPE of Lepiota lateritia, BR).

Material studied: Rugosospora pseudorubiginosa: BOLIVIA. Prov. José Ballivian: along banks of Río Beni, S of Rurrenabaque at junction of Río Tuichi, ± 67°30'W, 14°25'S, 31 Mar 1990, Franco-M. 345 (LPB, NY); 7 Apr 1990, Franco-M. 383 (BR, COL, LPB, NY). BRAZIL. SANTA CATARINA: Porto Novo, 1928, Rick 589 (FH). COLOMBIA. DPTO. ANTIOQUIA: Mpio. de San Luis, Parque Natural de la región de Rio Claro, Saldarriaga 8 (HUA, XAL). COSTA

RICA. PROV. PUNTARENAS: Peninsula Osa, Río Sandalo, elev. 1-5 m, 21 Aug 1936, *Dodge and Goerger 9889* (FH); 24 Aug 1936, *Dodge and Goerger 10131* (FH); Pto. Jimenez, 25 Apr 1936, *Dodge 7704* (FH); 27 Apr 1936, *Dodge 7674* (FH). MEXICO. CHIAPAS: Selva Lacandona, Mpio. de Ococingo, camino Lacanja a Rió Cedro, *Chacón 1987* (XAL). VENEZUELA. Dto. Federal: Chichiviriche, 5 Jul 1958, *Dennis and Aristeguieta 1145* (HOLOTYPE of *Lepiota epicharis* var. *occidentalis*, K).

Distribution: In the Neotropics from Mexico to Brazil.

Discussion: The main differences between *Rugosospora pseudorubiginosa* and *R. ochraceobadia* are the size of the basidiospores (Guzmán *et al.*, 1989) and also the quality of the basidiospore ornamentation. In *R. ochraceobadia* the basidiospores reach up to 14 µm long and are rugose (Fig. 29c) while in *R. pseudorubiginosa* the basidiospores reach up to 10 µm and the ornamentation forms a reticulum (Figs 29a-b). The variations in size of pileus elements and cheilocystidia are not enough to characterize the species.

Singer (1949) transferred *Lepiota rubrosquamosa* Rick to *Leucoagaricus*, but comments on a type specimen were not given. Later, Singer (1953) reconfirmed the position of

Lepiota rubrosquamosa in Leucoagaricus based on authentic material collected in Brazil (FH, specimen not explicitly cited). He characterized the species as having dextrinoid, metachromatic, and reticulated basidiospores, hymeniform pileipellis, and lacking clamp connections. I examined the five specimens determined by Rick as Lepiota rubrosquamosa in FH and two additional collections housed in PACA. I found that only one specimen in FH (Rick 589) has a hymeniform pileipellis, dextrinoid, metachromatic, and reticulated basidiospores. However, it has conspicous clamp connections. This is likely the specimen cited by Singer (1953) which he transferred to Leucoagaricus. Unfortunately, a type specimen fitting Rick's (1920) protologue could not be located in PACA or FH. Nevertheless, Lepiota rubrosquamosa Rick sensu Singer is identical to R. pseudorubiginosa described above. Lepiota rubrosquamosa sensu Rick is some other taxon with basidiospores originally described as 4-5 x 3 μm.

Rugosospora was characterized by Heinemann (1973a, 1973b) as possessing clamp connections contrary to a report of their absence (Guzmán et al., 1989; Velásquez et al. 1991).

Singer (1975) considered Rugosospora as a possible synonym of Macrolepiota and in 1986, considered the genus as a possible synonym of Leucocoprinus pointing out that the only difference between both genera is the ornamentation of the basidiospores in Rugosospora (ignoring other microscopic characteristics). Guzmán and Bandala (1989) described R. pseudorubiginosa, a second species for the genus, from Mexico and Colombia extending the geographical distribution of the genus to the Neotropics and pointing out the mycofloristic relationship between Africa and South America. Based on the material I have examined, the distribution of R. pseudorubiginosa is extended to Costa Rica (Central America), Bolivia and Brazil (South America) (Fig. 30).

Because of the metachromatic basidiospores and free lamellae, Rugosospora belongs to the tribe Leucocoprineae in the Agaricaceae as placed by Heinemann (1973a, 1973b) and Guzmán (1989); it does not fit in tribe Lepioteae as placed by Velásquez et al. (1991) or in the Cystodermateae as placed by Guzmán and Guzmán-Dávalos (1992).

Cystolepiota Singer

Lilloa 25: 281. 1952

Type species: Cystolepiota constricta Singer in Singer and Digilio.

The genus Cystolepiota was created by Singer (in Singer and Digilio, 1952) for those species of Lepiota with inamyloid basidiospores and a pileipellis formed of sphaerocysts. This concept was modified by Singer and Clemencon (1972), and species with dextrinoid basidiospores were included. Although, confusion has arisen around the distiction between Cystoderma and Lepiota section Echinatae (Knudsen, 1978) these two taxa differ in the structure of the pileipellis. In Cystolepiota, the pileipellis is formed of loose sphaerocysts, while in Lepiota section Echinatae the pileipellis is formed by a trichodermium of cylindric to ±catenulate hyphae with globose terminal cells. These terminal cells are not easily detachable. In addition, Knudsen (1980) pointed out the presence of intermediate cells (oblong to ellipsoid cells but not true sphaerocysts) are found in Lepiota section Echinatae but not in Cystolepiota, while the presence of uninucleate basidiospores in Cystolepiota separates this genera from all others in Lepiota s.l.

Cystolepiota coquisorum Franco-Molano sp. nov.

Basidiosporis 5-6(8) x 3-4 µm necnon pleuro- atque cheilocystidiis ventricoso-rostratis notabilis; a speciebus neotropicalis Cystolepiota albogiva Singer, C. amazonica Singer, C. pottassiovirens Singer et C. eriophora (Peck) Knudsen pleurocystidiis necnon basidiosporis majoribus diversa.

Etymology: Named after the Coguis Indians.

FIGS. 31a-d.

Pileus 2 cm diam, convex-plane; surface dry, breaking in finely fibrillose squamules, grayish brown (6E6) at the center, paler (6D5) toward the margin, on whitish background; margin appendiculate, inrolled. Context 1.2 mm thick, whitish, unchanging. Lamellae free, close, ventricose, 2 mm broad, white with brown spots. Stipe 0.5-3 cm long, 2 mm wide, central, equal, whitish and smooth at the apex, fibrillose-squamulose and concolorous with the stipe toward the base. Annulus not seen.

Macrochemical test: not performed.

Basidiospores (Fig. 31a) white, in mass 5-6(8) x 3-4 µm ($\overline{Q}$ = 1.76), ellipsoid to subcylindrical in all views, hyaline in KOH, inamyloid in Melzer's reagent; spore wall thin, smooth. Basidia (Fig. 31b) elongate to short clavate, 4-sterigmate, hyaline, inamyloid, 13-17 x 6-8 µm. Pleurocystidia (Fig. 31c) scattered, ventricose, with an apical prolongation, 23-28 x 6-8 µm; apical prolongation up to 10 x 3 µm. Edge of lamellae with scattered cheilocystidia. Cheilocystidia (Fig. 31d) ventricose with an apical prolongation, 25-35 x 8-12 µm; apical prolongation up to 15 x 3 µm. Hymenophoral trama hyaline, inamyloid, with hyphae 3-9 µm broad, thin-walled, regularly arranged. Subhymenium pseudoparenchymatous, hyaline, up to 15 µm thick; with cells 5-7 µm. Pileus trama hyaline, inamyloid, parallel, radially arranged hyphae; hyphae 3-15 µm broad. Pileipellis (Fig. 31d) epithelial, formed of loose, subglobose to globose cells; cells yellowish brown in H_2O and KOH, thin-walled, up to 30 µm diam. Stipitipellis, at the apex of the stipe, of hyphae parallel and vertically oriented, yellowish in H_2O and KOH, thin-walled, 4-12 µm broad, toward the base covered with sphaerocysts similar to those forming the pileipellis. Clamp connections present.

Material studied: COLOMBIA. DPTO MAGDALENA: Mpio. de Guachaca, vertiente Rio Buritica, Sierra Nevada de Santa Marta, Pueblo de los indios Coguis "Coscunguena", ±2300 m, 17 Jun 1992, Franco-M. 987 (HOLOTYPE, COL).

Distribution: Sierra Nevada de Santa Marta, Colombia.

Discussion: This species is undescribed. It differs from the neotropical species, *Cystolepiota albogilva* Sing., *C. amazonica* Sing., *C. pottassiovirens* Sing., *C. cinereofusca* Sing. and from *C. eriophora* (Peck) Knudsen in having pleurocystidia and bigger basidiospores. So far, it is the only species of *Cystolepiota* collected in Colombia.

Lepiota Pers.: S. F. Gray

Nat. Arr. Brit. Pl. 1: 601. 1821.

Fusispora Fayod, Prodromo Ann. Sc. Nat., Bot. VII. 9: 351. 1889.

Lepiotula (Maire) Locquin:Horak, Beitr. Krypt.-flora der Schweiz 13: 337. 1968

Morobia Horak, Sydowia Beih. 8: 205. 1979.

Type species: Lepiota colubrina (Pers.) S. F. Gray [= Lepiota clypeolaria (Bull.: Fr.) Kummer]

The genus Lepiota s.s. includes species with lepiotoid or pluteoid habit, macroscopically characterized by having pileus surface dry, squamulose, scaly fibrillose, fibrillose or at times glabrous, often brightly colored. Lamellae free, thin, sometimes staining upon bruising, sometimes marginate. Stipe central, in some cases with a surface, or at least at the lower portion, similar to the surface of the pileus, otherwise glabrous or with scattered remnants of "universal veil." Annulus present but very often evanescent. Microscopically, the genus is characterized by having a pileipellis ranging from repent, trichodermial to hymeniform, but never with an epithelium nor with true sphaerocysts. Basidiospores ovoid, broadly ellipsoid, ellipsoid, fusoid, oblong, sometimes with a truncate base or, in two sections, Stenosporae and Cristatae), spurred; inamyloid, dextrinoid or amyloid in Melzer's reagent, in any case metachromatic in cresyl blue; spore wall smooth or finely ornamented, not affected by the treatment with ammonia and acetic acid; germ pore absent. Pleurocystidia rarely present. Cheilocystidia present. Clamp connections present or absent

Key to sections

1. Pileipellis trichodermial or of radially arranged, repent hyphae.
   2. Basidiospores ovoid, ellipsoid to amygdaliform, never fusoid or stenosporic.
      3. Basidiospores dextrinoid.
         4. Clamp connections present....................
            Sect. Ovisporae, p. 159
         4. Clamp connections absent.....................
            Sect. Anomalae, p. 181

3. Basidiospores amyloid..........................
Sect. Amylosporae (Species not known from Colombia)

2. Basidiospores fusoid, fusoid with truncate apex to spurred.

5. Basidiospores fusoid; pileipellis trichodermial or repent.

6. Pileipellis trichodermial, rarely repent, without subglobose or globose terminal elements..................
Sect. Lepiota, p. 152

6. Pileipellis trichodermial; subglobose or globose non detersile terminal elements present.

7. Basidiospores dextrinoid............
Sect. Echinatae (Species not known from Colombia)

7. Basidiospores amyloid...............
Sect. Amyloidae (Species not kown from Colombia)

5. Basidiospores spurred; pileipellis trichodermial..............................
Sect. Stenosporae, p. 168

1. Pileipellis hymeniform.

8. Basidiospores ovoid, ellipsoid to amygdaliform but never fusoid or spurred............................
Sect. Lilaceae, p. 190

8. Basidiospores spurred...............................
Sect. Cristatae (Species not known from Colombia)

Section Lepiota

Clypeolariae (Fr.) Quél. 1872; Kühner, 1936.

Type species: L. clypeolaria (Bu ll.:Fr.) Kummer

Pileipellis trichodermial or of repent, radially arranged hyphae. Stipitipellis of parallel, vertically oriented hyphae often giving rise to tufts of hyphae similar to those forming the pileipellis. Basidiospores dextrinoid, fusoid, often with suprahilar depression. Clamp connections present.

Key to species found in Colombia

1. Pileus surface white, radially fibrillose; pileipellis of repent, radially arranged hyphae; basidia 2-sterigmata.. *L. bisporigera*, p. 153

1. Piles surface brown, fibrillose scaly; pileipellis trichodermial; basidia 4-sterigmata; basidiospores 9.9-11 x 3.6-4.5; cheilocystidia clavate to ventricose, often septate.. *L. theobromicola*, p. 156

Lepiota bisporigera Franco-Molano *sp. nov.*

Alba est, superficie fibrillose et quoque basidio sterigmatibus duobus proviso, ulterius sporis subfusiformibus vel fusiformibus haud metachromaticis insignis, *L. lacteam* Murrll et *L. colimensis* Murrill, quae basidosporis ovideis 4-sterigmatosis diversas, aliter simulans.

Etymology: The basidia of this species are characterized by having two sterigmata.

FIGS. 32a-d.

Pileus 1-1.6 cm diam, convex, plane, umbonate; surface dry, covered with fibrillose to strigose hairs radiating from disc, appearing slightly silky, pure white to yellowish (4A2) overall; margin appendiculate. Context less than 1 mm thick, white, unchanging when cut or bruised; Odor disagreable, taste not distinctive. Lamellae free, close, 2 mm broad, thin, white; margin entire, not marginate. Stipe 2-5.2 cm long, ± 1 mm diam, fleshy, equal to very slightly clavate, central; surface dry, silky, fibrillose with lens, whitish (7B2) at the apex, and yellowish grey at the base or yellowish grey overall, annulate. Annulus superior, descendent, membranous, concolorous with stipe surface, evanescent.

Macrochemical tests: not performed.

Basidiospores (Fig. 32a) (9.9)10.8-13.5 x 4.5-5.4 μm ($\overline{Q}$ = 2.63), fusiform to subcylindric in face view, subcylindric, broadly fusiform to fusiform with suprahilar depression in profile, hyaline in KOH, strongly dextrinoid in Melzer's reagent, not metachromatic in Cresyl blue. Basidia (Fig. 32b) clavate, 2-sterigmata, rarely 1-sterigmata, hyaline, inamyloid, 18-22.5(30) x 6.3-9(11) μm. Pleurocystidia absent. Edge of lamellae sterile with crowded cheilocystidia. Cheilocystidia (Fig. 32c) ventricose to narrowly utriform, 20-31 x 6.3-9 μm.

Hymenophoral trama hyaline, inamyloid, formed of cylindric to inflated hyphae of 2.7-10.8 µm, regular. Subhymenium pseudoparenchymatous, up to 10.8 µm thick; cells 6-12 µm broad. Pileus trama hyaline, inamyloid, parallel to interwoven but radially arranged; hyphae cylindric, thin-walled, 4.5-13.5 µm broad, thin-walled. Pileipellis (Fig. 32d) repent to semierect, formed of parallel, radially oriented, cylindric hyphae; hyphae, hyaline, inamyloid, thin-walled, smooth, often branched, with well-defined terminal cells; terminal cells clavate, ventricose, cylindric to pyriform, 2.7-14.5 µm broad. Stipitipellis hyphae parallel and vertically oriented, hyaline, inamyloid, thin-walled, 1.8-10.8 µm broad. Annulus tissue formed of interwoven, cylindric hyphae; hyphae branched or not, with clavate to ventricose terminal cells, hyaline, inamyloid, up to 10 µm broad. Clamp connections present.

Material studied: COLOMBIA. DPTO. CAUCA: Mpio. de Tunia, Corregimiento El Mango, km 93 de la carretera Cali-Popayán, Reserva Natural El Guayabo, 2°41′N 76°32′W, bosque mixto con Quercus humboldtii, 1640 m, 19 May 1987, G. Mueller, B. Strack and R. Halling (G. Mueller 2864) (F). COLOMBIA: same locality, 16 Nov 1988, Franco-M. 137 (HOLOTYPE, COL; ISOTYPE, NY).

Distribution: Known only from El Guayabo, Cauca, Colombia.

Discussion: Despite the white color and the fibrillose (not scaly) pileus surface this species does not belong in *Sericeomyces* because it has clamp connections, and its basidiospores are not metachromatic. The combination of characters, that include a repent epicutis, subfusiform to fusiform basidiospores, and the presence of clamp connections, make it difficult to place this species within a section. The fusiform basidiospores excludes it from section *Ovisporae*. Although, species belonging to section *Lepiota* have been described as having a trichodermial pileipellis, I include the species here because of its fusiform basidiospores and the presence of clamp connections. *Lepiota lactea* Murrill and *L. colimensis* Murrill were described as having pure white basidiomata, but they differ from *L. bisporigera* in having basidia with 4-sterigmata, ovoid basidiospores, and lack clamp connections. So far, none of the species of *Lepiota* s.s. have been described as having basidia bearing 2-sterigmata.

Lepiota theobromicola Franco-Molano *sp. nov.*

Lepiotam clypeolariam (Bull.:Br.) Kummer simulans, sed ab ea basidiosporis minoribus (9.9-11) x 3.6-4.5, nec 12-16 x 8-14 µm) cheilocystidiisque majoribus (20-40 x 8-14, nec 15-225 x 8-11 µm) diversa.

Etymology: The species was found on soil in a cacao plantation.

FIGS. 33, 34a-d.

Pileus 2 cm diam, convex; surface dry, entire at the center, fibrillose scaly toward the margin, center and scales brown (7D7) on white background; margin inrolled. Context 2 mm thick, white, unchanging when exposed. Odor strong, fungoid. Lamellae free, close, 3 mm broad, white, unchanging when bruised; margin entire, not marginate. Stipe 6 cm long, 3 mm wide, equal; surface flocose-fibrillose, with scattered fibrillose scales similar to those forming the pileipellis, whitish near the apex, pale orange (5A3-5A4) toward the base, annulate. Annulus superior, fibrillose, concolorous with stipe surface, evanescent.

Machrochemical tests: positive for tyrosinase throughout basidioma, positive for laccase throughout basidioma.

Basidiospores (Fig. 34a) white in mass, (8.1)9.9-11 x (2.7)3.6-.45 µm ($\overline{Q}$ = 3.05), subcylindrical in face view, fusoid with well defined suprahilar depression in profile, hyaline in KOH, dextrinoid in Melzer's reagent. Basidia (Fig. 34 b) clavate, 4-sterigmata, hyaline, inamyloid, 23-30 x 7-8 µm. Pleurocystidia absent. Edge of lamellae sterile with abundant cheilocystidia. Cheilocystidia (Fig. 34c) narrowly clavate, clavate to ventricose, often septate, 20-40 x 8-14 µm. Hymenophoral trama hyaline, inamyloid, regular, formed of cylindric to slightly inflated hyphae; hyphae 3-13 µm broad. Subhymenium pseudoparenchymatous, up to 30 µm thick; cells 5-15 µm diam. Pileus trama hyaline, inamyloid, formed of interwoven but radially oriented hyphae; hyphae cylindric to ±inflated, 5-15 µm broad. Pileipellis (Fig. 34d) a two-layered trichodermium, yellowish in KOH; the basal layer is formed of densely interwoven hyphae; hyphae cylindric with well-defined terminal cells; terminal cells clavate to ventricose, 10-15 µm broad. The basal layer gives rise to a second layer formed of long aseptate hyphae with acute to round ends, up to 250 x 7-16 µm. Stipitipellis at the apex of the stipe formed of hyphae parallel and vertically oriented, 7-15 µm broad, and by tufts of hyphae similar to those forming the pileipellis at the base. Annulus formed of a tissue similar to that tissue forming the apex of the stipe. Clamp connections present.

Material studied: COLOMBIA. DPTO. ANTIOQUIA: Mpio. de Támesis, vereda San Isidro, Finca El Chaleco, sobre suelo en cultivo de cacao, 1300 m, 11 Jun 1991, Franco-M. 742 (HOLOTYPE, COL).

Distribution: Known from Tamesis in the Dpto. de Antioquia, Colombia.

Discussion: This is an undescribed species, closely related to *Lepiota clypeolaria* from which differs in having smaller basidiospores and larger cheilocystidia. The basidiospores of *L. theobromicola* are 9.9-11 x 3.6-4.5 µm and the cheilocystidia are clavate to ventricose, often septate, and 20-40 x 8-14 µm. *Lepiota clypeolaria* has basidiospores 12-16 x 5-6 µm with clavate to sphaeropedunculate cheilocystidia measuring 15-25 x 8-11 µm.

Section Ovisporae (Lange) Kühner, Bull. Soc. Mycol. France 52: 190. 1936.

Type species: *Lepiota subincarnata* Lange

Pileus squamose, fibrillose-scaly, or at times smooth and glabrous. Stipe surface typically fibrillose but sometimes similar to the surface of the pileus.

Pileipellis trichodermial or of repent hyphae. Stipitipellis formed of parallel, vertically oriented hyphae, or sometimes similar to the pileipellis. Basidiospores cylindric, ellipsoid, ovoid to amygdaliform, never fusoid or spurred, dextrinoid. Clamp connections present.

Key to species found in Colombia

1. Pileus not exceeding 2 cm diam; pileus surface of brown squamules on white background; pileipellis of repent to semierect hyphae with very thick walls.................
L. bettinae, 161

1. Pileus at least 2 cm diam; pileus surface matted fibrillose or squamulose, brown on light brown or white background; pileipellis a cutis or a trichodermium of hyphae with thin walls.

    2. Pileus surface matted fibrillose, smooth; pileipellis or repent hyphae; basidiospores cylindric to ellipsoid, 6.3-8.1 x 2.7 μm; cheilocystidia clavate to sphaeropedunculate, usually septate......................................
    L. narinyensis, p. 163

2. Pileus surface squamulose; pileipellis of repent to semierect hyphae giving rise fascicles of terminal cells; basidiospores oblong to cylindric, 4.6-5.5 x 2.7 μm; cheilocystidia clavate, aseptate........... <u>L. azalearum</u>, p. 166

<u>Lepiota bettinae</u> H. Dörfelt, Zeitschr. Mykol. 48: 245-251. 1982.

FIGS. 35, 36a-d.

Pileus 0.2-1 cm diam, convex with small umbo, plane to uplifted; surface dry, finely squamulose; squamules 7E8, more abundant at the center, scattered toward the margin on whitish background; margin sligthtly appendiculate to entire. Context less than 1 mm thick, pale yellow (3A2), unchanging. Lamellae free, close, 3A2, margin entire. Stipe 0.5-1.5 cm long, less than 1 mm wide, brownish overall, finely squamulose; squamules concolorous, with white mycelium at the base. Annulus superior, arachnoid, concolorous with pileus surface.

Macrochemical test: not performed.

Basidiospores (Fig. 36a) 4-6 x 3-4 μm ($\overline{Q} = 1.61$), ellipsoid to broadly ellipsoid in face view, ellipsoid in profile, hyaline, dextrinoid. Basidia (Fig. 36b) clavate to broadly clavate, 4-sterigmata, hyaline, inamyloid, 14-20 x 6-7 μm. Pleurocystidia absent. Cheilocystidia (Fig. 36c) crowded, clavate to ventricose, 20-30 x 7-8 μm. Hymenophoral trama hyaline, inamyloid, with hyphae 4-10 μm broad, thin walled, regularly arranged. Subhymenium not very well differentiated from the trama, parenchymatous, up to 7 μm thick. Pileus trama hyaline, inamyloid, interwoven but radially arranged, with hyphae 3-10 (15) μm broad, thin-walled. Pileipellis reddish brown in KOH, formed of repent to erect, thick-walled hyphae (Fig. 36d); terminal cells cylindric to narrowly clavate, 30-70 x 3-8 μm. Stipitipellis consisting of hyphae parallel and vertically oriented, 2-7 μm broad, giving rise to patches of repent to semierect, very thick-walled hyphae similar to those forming the pileipellis. Clamp connections present.

Material studied: BOLIVIA. DPTO. DE BENI: Prov. José Ballivian, along banks of Rio Beni, S of Rurrenabaque and junction of Rio Tuichi, approx. 67° 30′ W, 14° 25′ S, 4 Apr 1990, Franco-M. 364a (LPB, NY); COLOMBIA. DPTO MAGDALENA: Mpio. de Guachaca, Sierra Nevada de Santa Marta, alto Buritica, 1800-2000 m, 16 Jun 1992, Franco-M. 977 (COL, NY). GERMANY: Halle/S., Botanischen Garten, 17 Mar 1981, Kieler und Dörfelt s.n (ISOTYPES: K, NY)

Distribution: It seems that Lepiota bettinae is a tropical species described from a greenhouse in Germany, where it was associated with tropical cultivated plants. It has been collected in Colombia and Bolivia.

Discussion: This small species is characterized by the thick-walled hyphae forming the pileipellis and stipitipellis. It grows gregariously in wet soil among grasses and ferns.

Lepiota narinyensis Franco-Molano sp. nov.

Ab omnibus sect. Ovisporarum speciebus pilei superficie fibrillose differt.

Etymology: Named for the Department of Nariño, Colombia.

FIGS. 37a-d.

Pileus 5 cm diam, broadly convex; surface dry, shiny, innately appressed fibrillose, with brown (7E7) appressed squamule-like patches on light brown (7D5) ground; margin inrolled. Context 3 mm thick, white, unchanging when exposed. Odor of benzaldehyde, taste mild benzaldehyde. Lamellae free, close, narrow (3 mm broad), ±thick, white;

margin entire to finely serrulate, not marginate. Stipe 8 cm long, 4 mm broad, central, equal; surface dry, woolly-fibrillose, white at the apex, light brown (7D6) below, annulate; interior white, hollow at the center. Annulus superior, fibrillose, concolorous with the stipe surface, evanescent. White rhizomorphs at the base.

Macrochemical tests: not performed.

Basidiospores (Fig. 37b) (5.4)6.3-8.1(9.3) x 2.7(3.6) µm ($\overline{Q}$ = 2.53), cylindric to ellipsoid with round base in facial view, cylindric to ellipsoid with round base, often with suprahilar depression in profile, hyaline in KOH, dextrinoid in Melzer's reagent, not metachromatic in Cresyl blue; spore wall thin, smooth. Basidia (Fig. 37c) clavate, 4-sterigmata, hyaline, inamyloid, 17.6-22 x 4.5-6.3 µm. Pleurocystidia absent. Edge of lamellae sterile with crowded cheilocystidia. Cheilocystidia (Fig. 37a) vesiculose, broadly clavate, subpiriform, turbinate, cylindric or sphaeropedunculate, usually 1-3 (sometimes more) septate, 23-62 x 9-20 µm. Hymenophoral trama hyaline, inamyloid, with hyphae cylindric to inflated, up to 12 µm broad, thin-walled, regularly arranged. Subhymenium pseudoparenchymatous, ±15 µm thick; cells 5-8 µm diam. Pileus trama very pale yellow to hyaline in KOH, inamyloid, formed of cylindric, parallel hyphae but radially arranged, up to 12 μm broad. Pileipellis (Fig. 37d) composed of repent hyphae, radially arranged; hyphae hyaline to yellowish in KOH, cylindric, up to 14 μm broad. Stipitipellis formed of parallel, vertically oriented hyphae; hyphae pale yellow to almost hyaline near the apex, and darker toward the base, up to 7 μm broad. Annulus formed of hyphae similar to those at the apex of the stipe, parallel to interwoven. Clamp connections present.

Material studied: COLOMBIA. DPTO. NARINO: Mpio. de Pasto, Laguna La Cocha, Isla La Corota, 30 km E of Pasto, mixed forest, 2760 m, 21 Nov 1988, Franco-M., R. Halling, D. Desjardin, O. Salazar (Franco-M. 179) (HOLOTYPE, COL; ISOTYPE, NY).

Distribution: Known only from La Corota, Pasto, Colombia.

Discussion: The matted fibrillose pileus surface of this species seems to be unique. Although Lepiota guatopoensis, L. roseolamellata, and L. pseudoroseola were described (Pegler, 1983) as having smooth and glabrous pilei, L. pseudoroseola has been transferred to Leucoagaricus (Heinemann, 1973), and L. guatopoensis and L. pseudoroseola have a finely fibrillose pileus surface, and lack clamp connections. Lepiota subamanitiformis also has smooth pileus and larger basidiospores (7-8 x 4.5-5 µm).

Lepiota azalearum (Murrill) Dennis, Kew Bull. 7: 474. 1952.

FIGS. 38, 39a-e.

≡ Cortinellus azalearum Murrill, Lloydia 5:131. 1942.

Pileus up to 2 cm diam, plano-convex with a low umbo; surface recurved fibrillose scaly; scales light brown (7D6) on white background, more concentrated at the center; margin entire, sterile, projecting, inrolled. Context ±1 mm thick, white, unchanging. Odor very strongly farinaceous. Lamellae free, ±remote from the stipe, close, 1.5 mm broad, white, unchanging when bruised; margin entire, not marginate. Stipe 3 cm long, 2 mm wide, equal, central; surface dry, glabrous, whitish with few brown fibrillose scales at the base, annulate. Annulus ±central, white with pale brown (7D6) edge, membranous, ascendent, evanescent.

Macrochemical tests: positive for tyrosinase throughout basidioma; negative for laccase.

Basidiospores (Fig. 39a) (3.7)4.6-5.5(6.5) x (1.8)2.7 µm ($\overline{Q}$ = 1.86), oblong to cylindric in face view and in profile, dextrinoid. Basidia (Fig. 39b) clavate, 4-sterigmata, at times 2-3-sterigmata, 15.8-8.6 x 4.6-7.4 µm, hyaline, inamyloid. Pleurocystidia absent. Edge of lamellae with abundant cheilocystidia. Cheilocystidia (Fig. 39c) clavate, 18.6-20.5 x 6.5-8.4 µm. Hymenophoral trama hyaline, inamyloid, with hyphae up to 10 µm broad, regularly arranged. Subhymenium pseudoparenchymatous, 8-10 µm thick; cells up to 8 µm diam. Pileus trama hyaline, inamyloid, parallel to interwoven but with radial orientation, hyphae up to 20(25) µm broad. Pileipellis consisting of interwoven, repent to erect, mostly branched hyphae; hyphae brownish in KOH, ±5 µm broad, giving rise to fascicles of terminal cells (Fig. 39d); terminal cells clavate to cylindric with round to acute ends, 30-160 µm long x 6-22 µm broad. Stipitipellis composed of vertically oriented, parallel hyphae, 2-8 µm broad. Annulus formed of parallel radially oriented hyphae in its inner side and of hyphae similar to those forming the pileilipellis (Fig. 39e) in its outer side. Clamp connections present.

Material studied: COLOMBIA. DPTO. META: Mpio. de San Luís de Cubarral, bosque mixto muy húmedo, 480 m, 31 May 1991, Franco-M. 717 (COL, NY). MARTINIQUE. Precheur:

Hauter Anse Couleuvre, on very rotten wood, 20 Sep 1977, Pegler 2814 (K). TRINIDAD. Erin: on ground in secondary bush, 6 Nov 1949, Dennis 306 (K).

Distribution: Antilles and in the Dpto. Meta, Colombia.

Discussion: Even though no pyriform cheilocystidia were observed, this collections fits the description of *L. azalearum* by Pegler (1983). However, the type of *Cortinellus azalearum* at FLAS, needs re-examination for further comparison and more accurate observations.

Section Stenosporae (Lange) Kühner, Bull. Soc. Mycol. France 52: 194. 1952.

Type species: *Lepiota pseudofelina* Lange

Pileus surface squamulose. Pileipellis trichodermial. Stipe surface usually similar to the pileus surface at least below the annulus. Stipitipellis similar to pileipellis. Basidiospores dextrinoid, spurred or at least strongly truncate at the base. Spore wall thin, smooth to sligtly ornamented. Clamp connections present.

Key to species found in Colombia

1. Pileus with brown squamules on white or sulphur yellow background; basidiospores above 9 μm long.

    2. Pileus with brown squamules on white background; context and lamellae white, not changing when bruised.

        3. Spore wall smooth; basidiospores 9-11 x 3.6-4.5 μm.. <u>L. pseudoignicolor</u>, p. 178

        3. Spore wall finely papillate ornamented; basidiospores 9-11 x 2.7-11...................... <u>L. papillata</u>, p. 173

    2. Pileus with brown squamules on sulphur yellow background; context and lamellae sulphur yellow staining blue green on bruising.................... <u>L. sulphurocyanescens</u>, p. 175

1. Pileus with dark vinaceous squamules on white background; pileipellis terminal cells 12-100 x 3-10 μm; basidiospores 4.5-9 x 2.7-3.6 μm...................... <u>L. erythrosticta</u>, p. 170

Lepiota erythrosticta (Berk. & Br.) Sacc., Syll. Fung. 5: 62. 1887.

FIGS. 40, 41a-d.

≡ Agaricus erythrostictus Berk. & Br., J. Linn. Soc., Bot. 11: 508. 1871

Pileus 0.6-2.4 cm diam, convex to mammillate; surface dry, greyish red (10D5) to vinaceous, entire to minutely squamulose at the center, disrupting into small squamules toward the margin; margin entire to appendiculate, at times inrolled, non-striate. Context thin (less than 1 mm thick), white, unchanging when cut or bruised. Odor and taste not distinctive. Lamellae free, ±remote from the stipe, close, narrow (±1 mm broad), whitish to pinkish, unchanging when bruised; margin entire, not marginate. Stipe 3-4 cm long, 1-2 mm wide, central, equal; suface dry, scurfy squamulose, pinkish (8A2) at the apex, concolorous with the pileus toward the base, annulate. Annulus superior, ascendent, fibrillose, concolorous with stipe surface, evanescent.

Macrochemical tests: Not performed.

Basidiospores (Fig. 41a) (4.5)5.4-8.1(9) x 2.7-3.6 μm ($\overline{Q}$ = 1.98), ovoid to broadly ellipsoid in face view, spurred in profile, hyaline to yellowish in KOH, dextrinoid in Melzer's reagent, not metachromatic in Cresyl blue. Basidia (Fig. 41b) clavate, 4-sterigmata, rarely 2-sterigmata, hyaline, inamyloid, 15-22.5 x 6.3-7.2 μm. Pleurocystidia absent. Edge of lamellae sterile with crowded cheilocystidia. Cheilocystidia (Fig. 41c) cylindric, clavate, ventricose, thin-walled, 20-30 x 5-10 μm. Hymenophoral trama hyaline, inamyloid, with hyphae up to 8 μm broad, regularly arranged. Subhymenium pseudoparenchymatous, 8-14(18) μm thick; cells 5-26 μm broad. Pileus trama hyaline, inamyloid, parallel to interwoven but radially arranged, with hyphae of 3-10 μm broad. Pileipellis a trichodermium formed of hyphae with well-defined terminal cells; terminal cells (Fig. 41d) narrowly clavate to fusoid, rarely septate appearing catenulate, pale red in water, reddish-brown to yellowish or with yellowish contents in KOH, 12-100 x 5-14 μm. Stipitipellis composed of hyphae hyaline, yellowish to very pale reddish-brown in KOH, with well-defined terminal cells; terminal cells clavate to ventricose, 15-80 x 9-14 μm. Annulus formed of a tissue similar to the tissue forming the stipitipellis and pileipellis. Clamp connections present.

Material studied: BOLIVIA. Prov. José Ballivian: along banks of Río Beni, S of Rurrenabaque at juction of Río Tuichi, ±67°30'W, 14°25'S, 7 Apr 1990, Franco-M. 385 (LPB, NY); Prov. Iturralde: N of Rurrenabaque, along Río Beni, pueblito Capaina, ±67°30'W, 14°20', 10 Apr 1990, Franco-M. 397 (LPB). COLOMBIA. DPTO VALLE: Mpio. de Zarzal, Hacienda el Medio, entre Zarzal y Paila, 940-950 m. 14 Nov 1988, Franco-M. 131 (NY). CUBA. Prov. de Matanzas: near Matanzas, on leaf-mould, 9 Sep. 1903, N. L. Britton and P. Wilson 398 (NY). SRI LANKA: Peradineya, on the ground, Sep 1868, Thwaites 755 (HOLOTYPE, K).

Distribution: This species was originally described from Sri Lanka, but it has also been reported from the Lesser Antilles (Pegler, 1983) and New Guinea (Horak, 1980b). In this work its distribution is extended to Bolivia and Colombia.

Discussion: The vivid pink to vinaceous color of the basidiomata, the size and shape of the basidiospores, the size and shape of the cheilocystidia, and pileipellis structure make it easy to identify this species. The macro- and microscopic features of the studied material fit with the description of *Lepiota erythrosticta* in Pegler (1983). Although, Horak (1980b) pointed out that Pegler's description does not correspond to *L.*

erythrosticta proper, my examination of tiny fragments of type material indicate that Pegler's description fits.

Lepiota papillata Franco-Molano, sp. nov.

Ob basidiosporas calcaratas et pileipellem trichodermalem sect. Stenosporis referenda, sed basidiosporis papillato-ornatis ab aliis sectionis speciebus diversa.

Etymology: The basidiospores of this species are papillate ornamented.

FIGS. 42, 43a-e, 44.

Pileus 0.2-1.2 cm diam, convex to plane; surface dry, finely squamulose; squamules yellowish brown (7E8) when young, paler (7C7) when mature on white background; margin entire to appendiculate. Context 2 mm thick, white, unchanging when exposed. Odor and taste strongly farinaceous. Lamellae free, close, 2 mm broad, white, unchanging when bruised, not marginate; margin finely serrate. Stipe 0.7-3 cm long, ± 1 mm wide, central, equal; surface dry, fibrillose, white overall or yellowish brown at the base, with scattered yellowish brown (7E8) squamules similar to those on pileus. White rhizomorphs at the base. Annulus superior, fibrillose, concolorous with pileus surface, evanescent.

Macrochemical tests: not performed

Basidiospores (Fig. 43b) (8.1)9-11 x 2.7-36 μm, ($\bar{Q}$ = 2.79), cylindric to subcylindric in face view, spurred in profile, hyaline in KOH, dextrinoid in Melzer's reagent; spore wall finely papillate ornamented (Fig. 44). Basidia (Fig. 43d) narrowly clavate to clavate, 4-sterigmata, rarely 2-3-sterigmata, hyaline, inamyloid, 27-30 x 7-9 μm. Pleurocystidia absent. Edge of lamellae sterile with crowded cheilocystidia. Cheilocystidia (Fig. 43a) cylindric, ventricose, utriform to narrowly utriform, 20-34 x 5-7 μm. Hymenophoral trama hyaline, inamyloid, regular, formed of cylindric to inflated hyphae of 3-12 μm broad. Subhymenium pseudoparenchymatous, 10-15 μm thick. Pileus trama hyaline, inamyloid, with hyphae parallel to loosely interwoven but radially oriented, cylindric to inflated, 2-16(20) μm broad. Pileipellis a trichodermium of cylindric hyphae, branched or not, with well-defined terminal cells, yellowish to brownish in H_2O and KOH; terminal cells (Fig. 43e) cylindric, ventricose to clavate, up to 160 x 12 μm. Stipitipellis hyphae parallel and vertically oriented, 2-12 μm broad, giving rise to densely interwoven cylindric hyphae with ventricose to clavate terminal cells; terminal cells (Fig. 43c) similar to those forming the pileipellis; yellowish in KOH, 20-100 x 8-15 µm. Clamp connections present.

Material studied: COLOMBIA. DPTO. AMAZONAS: Mpio. de Nariño, Isla Mocagua, 1 May 1992, Franco-M. 798 (HOLOTYPE, COL).

Distribution: Known only from the Island of Mocagua, Amazonas, Colombia.

Discussion: Because of the spurred basidiospores and the trichodermial pileipellis, this species belongs to section *Stenosporae*. However, it differs from the other species of the section in having papillate ornamented basidiospores (Fig. 44). This is the only species of *Lepiota* s.s. with ornamented basidiospores.

Lepiota sulphureocyanescens Franco-Molano *sp. nov.*.

Ab aliis *Lepiotae* speciebus (*L. coerulescens* Peck, *L. cyanescens* Beelii, *L. cyanozonata* Longear et *L. cyanea* Rick) cyanescentibus basidiosporis calcaratis differt.

Etymology: Meaning that the sulphur color of this species becomes blue when bruised or exposed.

FIGS. 45a-e.

Pileus up to 2.5 cm diam, convex to plano-convex; surface dry, brown, entire at the center, splitting in irregularly distributed scales toward the margin on sulphur yellow background. Lamellae free, close, sulphur yellow, staining blue green when bruised. Stipe 2-5.5 cm long, surface fibrillose, sulphur yellow overall or at times with scattered brown fibrillose scales, annulate. Cottony mycelium at the base. Annulus superior, fibrillose, sulphur yellow, evanescent.

Macrochemical tests: not performed.

Basidiospores (Fig. 45c) 6.3-10.8 x ± 3.6 µm ($\overline{Q}$ = 2.5), cylindric to oblong with a protracted base in face view, spurred in profile, hyaline in KOH, dextrinoid in Melzer's reagent. Basidia (Fig. 45b) narrowly clavate, 4-sterigmata, yellowish in KOH and water, inamyloid in Melzer's reagent, 25-33(38) x 7-10 µm, often buried in the subhymenium. Pleurocystidia absent. Edge of lamellae with crowded cheilocystidia. Cheilocystidia (Fig. 45a) cylindric to narrowly clavate, 20-33 x 5-8 µm. Hymenophoral trama hyaline, inamyloid, with hyphae 3-6 µm broad, regularly arranged. Subhymenium pseudoparenchymatous, ±10 µm thick; cells 4-6 µm diam. Pileus trama radially oriented and parallel, yellowish in water, hyaline to yellowish in KOH, inamyloid, formed of cylindric to vesiculose hyphae, 6-15 µm broad. Pileipellis yellowish in KOH, inamyloid, formed of dense interwoven, repent to erect, septate, cylindric hyphae with cylindric, clavate to ± pyriform terminal cells; terminal cells (Fig. 45d) septate or not, thin-walled, 25-60 x 6-15 µm. Stipitipellis of parallel and vertically oriented hyphae, 2-17 µm broad, thin-walled. Annulus formed of two differrent tissues: the inner side formed of densely interwoven, cylindric hyphae, yellowish in KOH, up to 7 µm broad; the outer side formed of hyphae similar to those forming the pileipellis (Fig. 45e), sometines with a dense, yellow or greenish content; terminal cells up to 70 x 25 µm. Clamp connections present.

Material studied: COLOMBIA. DPTO. QUINDIO: Mpio. de Salento, estación La Montaña, Alto Quindio, 2900 m, 12 Junio 1991, A. Peñuela and L. G. Henao 742 (HOLOTYPE, COL; ISOTYPE, NY).

Distribution: Known from the Dpto. de Quindio, Colombia.

Discussion: Of the species of *Lepiota* (*L. coerulescens* Peck, *L. cyanescens* Beeli, *L. cyanozonata* Longyear, *L.*

cyanea Rick) that stain blue when bruised or exposed, L. sulphurocyanescens is unique in having spurred basidiospores.

Together with L. gangrei (Eyre) Kühner, L. pseudofelina Lange, and L. griseovirens Maire, this species belongs to the group of greenish species (Vellinga and Huijser, 1993). While L. sulphurocyanescens turns blue and has a pileipellis formed of cylindric elements with clavate terminal cells, L. gangrei, L. pseudofelina, and L. griseovirens turn orange-brown and the pileipellis are formed of cylindric elements.

Lepiota pseudoignicolor Dennis, Kew Bull., 15: 115. 1962

FIGS. 46, 47a-d.

≡ Lepiota subgranulosa var. majus Dennis, Kew Bull. 7: 428. 1952.

Pileus up to 1.7 cm diam, convex, umbonate to plane with a low umbo; surface dry, with scurfy reddish brown (8D8) scales, more concentred at the center on white background; margin inrolled to decurved, slightly projecting. Context thin (± 1mm thick), white becoming pale brown with age. Odor mild, unpleaseant. Lamellae free, close, up to 1.2 mm broad, white, becoming pale brown with age; margin even, not marginate. Stipe 2.5 to 5 cm long, less than 1 mm wide, central, equal; surface whitish at the apex, reddish brown (8D8) toward the base, glabrous or at times with scattered scales similar to those on pileus; interior hollow, concolorous with the surface. White mycelium at the base. Annulus superior to central, concolorous with stipe surface, fugacious.

Macrochemical tests: not performed.

Basidiospores (Fig. 47a) white in mass, (8.1) 9-11 (13.5) x 3.6-4.5 µm ($\bar{Q}$ = 2.55), cylindric to oblong with a protracted base in face view, spurred in profile, hyaline in KOH, dextrinoid in Melzer's reagent. Basidia (Fig. 47b) clavate, 4-sterigmata, hyaline in KOH, inamyloid in Melzer's reagent, 23-27 x 7-8 µm. Pleurocystidia absent. Edge of lamellae sterile with abundant cheilocystidia. Cheilocystidia (Fig. 47c) cylindric to clavate, rarely septate, 23-35 x 6-8 µm. Hymenophoral trama hyaline, inamyloid, with hyphae 3-10 µm broad, thin-walled, regularly arranged. Subhymenium pseudoparenchymatous, 7-10 µm thick; cells up to 10 µm diam. Pileus trama radially oriented and interwoven, hyaline, inamyloid, with hyphae 3-6 µm broad. Pileipellis formed of interwoven, repent to erect, cylindric to narrowly clavate hyphae at the base, giving rise to a trichodermium of terminal cells; terminal cells (Fig. 47d) clavate to cylindric, brownish in H_2O and KOH, thin-walled, 30-180 x 5-12 μm. Stipitipellis formed of hyphae parallel and vertically oriented, 4-10 μm broad, giving rise to loosely interwoven hyphae with terminal cells similar to those of the pileipellis. Annulus tissue formed of interwoven cylindric hyphae with terminal cells similar to those of pileipellis. Clamp connections present.

Material studied: COLOMBIA. DPTO. ANTIOQUIA: Mpio. de Jardín, vereda Quebrada Bonita, bosque a orilla de la carretera hacia Riosucio, 1800 m, 7 Jun 1991, Franco-M. 727 (COL, NY); DPTO. QUINDIO: Mpio. de Salento, Estación La Montaña, Alto Quindio, 2900 m, 11 Jun 1991, A. Peñuela and L. G. Henao 711 (COL, NY). COSTA RICA. Prov. PUNTARENAS: Wilson Botanical Garden, west side trial, Quercus oocarpa, 10 Nov 1989, Franco-M. 317 (NY). VENEZUELA. CARACAS: Rio Chacaito, on soil in forest, 18 Nov. 1949, Dennis 351 (HOLOTYPE of L. pseudogranulosa var. majus, K); MERIDA: Sierra de Santo Domingo, 30 Jul 1958, Dennis and Buza 1752 (HOLOTYPE of L. pseudoignicolor, K).

Distribution: Neotropical. It has been previously reported from the Antilles (Pegler, 1983) and Venezuela (Dennis, 1962). In this work its distribution is extended to Colombia and Costa Rica.

Discussion: The type of Lepiota pseudoignicolor has 9-13 x 4-5 μm basidiospores and the terminal cells are cylindric to ventricose, up to 150 μm. Franco-M. 727 has smaller basidiospores and the terminal cells are cylindric to clavate. Peñuela and Henao 711 differs from the type in the presence of few aseptate terminal cells.

Section Anomalae Locquin, Bull. Mens. Soc. inn. Lyon 14: 93. 1945

Type species: L. fuscovinacea Möller & Lange

Pileus squamose, fibrillose-scaly, to radially fibrillose, or at times smooth and glabrous. Stipe surface typically fibrillose but sometimes similar to the surface of the pileus. Pileipellis trichodermial or of repent hyphae. Stipitipellis formed of parallel, vertically oriented hyphae, or sometimes similar to the pileipellis. basidiospores cylindric, ellipsoid, ovoid to amygdaliform, never fusoid or spurred, dextrinoid. Clamp connections absent.

Key to species found in Colombia

1. Pileus surface brown, squamulose to recurved fibrillose-scaly; pileipellis trichodermial; stipe surface similar to the surface of the pileus; lamellae marginate; basidiospores 8-10 x 3.6-4.5 µm.............
<u>L.</u> <u>belmirensis</u>, p. 182

1. Pileus surface orange or reddish-orange to reddish, radially fibrillose to finely tomentose; pileipellis of repent hyphae radially arranged; stipe surface finely fibrillose to glabrous; lamellae not marginate; basidiospores 5.4-8.1 x 3.6-4.1 µm.

   2. Pileus surface orange to orangish red, radially fibrillose to finely squamulose; basidiospores 6-7 x 3.6-4 µm ellipsoid to broadly ellipsoid; KOH on pileus negative....................................
   <u>L.</u> <u>guatopoensis</u>, p. 185

   2. Pileus surface reddish, tomentose to subtomentose; basidiospores 6.3-7.2 x 3.6-4.5 µm ellipsoid to amygdaliform; KOH on pileus yellowish........ ......
   <u>L.</u> <u>microcystidiata</u>, p. 188

<u>Lepiota</u> <u>belmirensis</u> Franco-Molano <u>sp.</u> <u>nov.</u>

Lepiotam ianthinosquamosam simulans, basidosporis minoribus, cheilocystidiis majoribus, hyphisque intus fusco-brunneis (nec, ut descripis, violaceis) diversa.

Etymology: Named for the Municipio de Belmira, Antioquia, Colombia,

FIGS. 48, 49a-e.

Pileus 2.5 to 3 cm diam, convex when young to plane with broad umbo with age; surface dry, reflexed squamulose, dark brown (6F8) overall; margin projecting, sterile, inrolled when young to decurved with age. Context 1-1.5 mm thick, white, unchanging, odor and taste not distinctive. Lamellae free, close, up to 2 mm broad, white, unchanging, marginate; margin of lamellae dark brown (6F8). Stipe 3-6 cm long, 1.5-2.5 mm wide near the apex, central, equal, strict to curved; surface dry, roughly tomentose, concolorous with pileus surface; interior stuffed, white, unchanging. Annulus superior, ascendent, membranous and white on the inner part, fibrillose as a continuation of the stipe surface outside, evanescent.

Macrochemical tests: positive for laccase on the base of the stipe; positive for tyrosinase on context of pileus and stipe; KOH on pileus, negative.

Basidiospores (Fig. 49b) white in mass, 8.1-10 (11) x 3.6-4.5 (5.4) µm, ($\overline{Q}$ = 2), broadly ellipsoid, oblong to cylindric in all views, hyaline in H_2O and KOH, dextrinoid in Melzer's reagent, not methacromatic in Cresyl blue. Basidia (Fig. 49c) broadly clavate, 4-sterigmata, hyaline, inamyloid, 25-35 x 9-11 µm. Pleurocystidia absent. Edge of lamellae sterile with crowded cheilocystidia. Cheilocystidia (Fig. 49a) ventricose, broadly clavate, clavate to cylindro-clavate, 30-60 x 10-18 µm. Hymenophoral trama hyaline, inamyloid, formed of clavate, broadly clavate to cylindro-clavate hyphae, up to 20 µm broad, regularly arranged. Hymenopodium well differentiate, formed of cylindric hyphae up to 4 µm. Subhymenium pseudoparenchymatous, 10-20 µm thick; cells up to 12 µm diam. Pileus trama hyaline, inamyloid, of densely interwoven but radially arranged hyphae; hyphae cylindric to inflated, 5-20 µm broad. Pileipellis (Fig. 49d) a trichodermium at the center, consisting of repent to erect hyphae toward the margin; hyphae with dark brown pigment in H_2O and KOH, often incrusted, branched or not, often with small diverticula, with cylindric to narrowly clavate terminal cells; terminal cells 5-15 (26) µm broad. Stipitipellis formed of parallel, vertically arranged, hyaline hyphae of 3-10 (15) µm broad, covered by hyphae with brown pigment and often incrusted similar to the hyphae forming the pileipellis with clavate terminal cells; terminal cells (Fig. 49e) of up to 180 µm long and up to 18(26) µm broad. Annulus formed of hyaline, cylindric, septate, branched or not, densely interwoven hyphae, up to 12 µm broad on the inner side and as a continuation of the stipitipellis on the outer side. Clamp connections absent.

Material studied: COLOMBIA. DPTO. ANTIOQUIA: Mpio. de Belmira, Finca Beltrucha, bosque mixto con algunos *Quercus*, 4 Jun 1992, Franco-M. 918 (HOLOTYPE, COL; ISOTYPE, NY)

Distribution: Known only from Mpio. de Belmira, Antioquia, Colombia.

Discussion: This species seems to be close to *Lepiota ianthinosquamosa* Pegler, however the latter has bigger basidiospores and smaller cheilocystidia. In addition, in *L. ianthinosquamosa* the hyphae of the pileipellis are described as having violaceous content while in *L. belmirensis* the content is dark brown.

Lepiota guatopoensis Dennis, Kew Bull. 15: 111. 1962.

FIGS. 50, 51a-d.

Pileus 0.8 cm diam, plane with low umbo; surface dry, radially fibrillose or, at times, squamulose, reddish orange (7B6) overall, darker at the center; margin decurved, entire. Context white, less than 1 mm thick, unchanging. Odor and taste mild. Lamellae free, close, up to 1 mm broad, white, unchanging; margin finely serrate. Stipe 2 cm long, ±1 mm wide, central, equal, glabrous, smooth, annulate. Annulus superior, ascendent, membranous.

Macrochemical tests: Negative for laccase; negative for tyrosinase; KOH on pileus, negative; NH_4OH on pileus, negative.

Basidiospores (Fig. 51b) white in mass, (5.4)6-7 x 3.6-4 µm ($\overline{Q}$ = 1.58), ellipsoid to broadly ellipsoid in face view, ellipsoid in profile, hyaline in KOK, dextrinoid in Melzer's reagent. Basidia (Fig. 51b) clavate to broadly clavate, 4-sterigmata, hyaline, inamyloid, 16-20 x 6-8 µm. Pleurocystidia absent. Edge of lamellae sterile with crowded cheilocystidia. Cheilocystidia (Fig. 51a) narrowly clavate, cylindro-clavate to cylindric, 43-50 x 7-8 µm. Hymenophoral trama hyaline, inamyloid, with hyphae cylindric to inflated, up to 15(20) µm broad, thin walled, regularly arranged. Subhymenium pseudoparenchymatous, ±12 µm thick; cells ±8 µm broad. Pileus trama hyaline, inamyloid, formed of densely interwoven cylindric hyphae; hyphae ±3 µm broad. Pileipellis a trichodermium at the center; formed of repent, semirect to erect, loosely interwoven hyphae toward the margin; hyphae (Fig. 51d) cylindric, septate, with an orange brown pigment in H_2O and KOH, often slightly incrusted, 5-15 µm broad. Stipitipellis of hyphae parallel and vertically oriented, 4-12 (20)µm broad, thin-walled. Annulus tissue of hyaline, densely interwoven hyphae, 3-5 µm broad. Clamp connections absent.

Material studied: BOLIVIA. Prov. Iturralde: N of Rurrenabaque, along Rio Beni, pueblito Capaina, approx. 67°30'W, 14°20', 5 Apr 1990, Franco-M. 372 (LPB). COLOMBIA. DPTO. CAQUETA: Mpio. de Salento, Inspección de Araracuara, parcela de Oscar Román, 8 May 1992, Franco-M. 842 (COL); DPTO. AMAZONAS: Parque Nacional Amacayacú, alrededores de la estación, 30 Apr 1993, Franco-M. 793 (COL). VENEZUELA. EDO. MIRANDA: Guatopo, on ground in forest, 800 m, 25 Jun 1958, Dennis 1106 (HOLOTYPE, K).

Distribution: Neotropical. It had been reported from the Antilles, Venezuela and Brazil. This work adds two new localities, Bolivia and Colombia, to the distribution of the species.

Discussion: The size of the basidiomata, the orange red, fibrillose pileus make it easy to recognize this species. However, microscopic variation in the shape and size of the cheilocystidia were observed, Franco-M. 842 differs from the type of *L. guatopoensis* in having narrower and larger cheilocystidia.

Lepiota microcystidiata Guzmán-Dávalos & Guzmán, Bull. Soc. Mex. Micol. 17: 47. 1982.

FIGS. 52a-d.

Pileus 7 mm diam, campanulate with a low umbo; surface dry, reddish, subtomentose to ±fibrillose. Context 1 mm thick, white. Stipe ±4.5 cm long, annulate. Annulus superior, ascendent, fibrillose, white with reddish edge, not evanescent.

Macrochemical tests: KOH yellowish on pileus.

Basidiospores (Fig. 52a) (5.4)6.3-7.2(8.1) x 3.6-4.5 µm ($\overline{Q}$ = 1.77), broadly ellipsoid to ovoid in face view, broadly ellipsoid to amygdaliform in profile, hyaline in KOH, dextrinoid in Melzers. Basidia (Fig. 52b) clavate, 4-sterigmata, hyaline, inamyloid, sometimes buried in the hymenophoral trama, 23-33 x 7-8 µm. Pleurocystidia absent. Cheilocystidia (Fig. 52c) crowded, not forming a sterile edge on lamellae, clavate, ventricose, somewhat utriform or constricted, 22-35 x 6-12 µm. Hymenophoral trama hyaline, inamyloid, with hyphae 3-10 µm broad, thin-walled, parallell to slightly interwoven. Subhymenium pseudoparenchymatous, 8-10 µm thick. Pileus trama radially oriented and parallel to slightly interwoven, hyaline, inamyloid, with hyphae 3-12 µm broad, thin walled. Pileipellis repent to semierect, consisting of slightly interwoven but radially oriented hyphae (Fig. 52d); hyphae hyaline, inamyloid, often branched or anastomosing, 3-10 µm broad, thin-walled. Stipitipellis consisting of hyphae parallel and vertically oriented, 2-12 µm broad, smooth, thin-walled. Annulus tissue formed of hyphae 5-12 µm broad, cylindric, septate, often branched, hyaline to yellowish in KOH. Clamp connections absent.

Material studied: COLOMBIA. DPTO. QUINDIO: Mpio. de Salento, estación La Montaña, Alto Quindio, 2900 m, 9 Jun 9, 1991, A. Peñuela and L. G. Henao 674 (COL, NY); 10 Jun 1991, A. Peñuela and L. G. Henao 700A (COL, NY).

Distribution: Neotropical, Mexico and Colombia.

Discussion: This species is very close to *L. guatopoensis* Dennis from which it differs in lacking incrusted hyphae in the pileipellis and in having smaller cheilocystida. In addition, the pileus surface of *L.*

guatopoensis is radially fibrillose while L. microcystidiata has been described as subtomentose. In the examined collection, the pileus turns yellow in KOH but this reaction is described from the type. Lepiota guatopoensis does not change with KOH.

Section Lilaceae M. Bon, Doc. Mycol. 43: 46. 1981.

Type species: Lepiota lilacea Bres.

Pileus surface breaking into small scales or areolae, remaining entire at the central "calotte." Pileipellis, at least at the center, hymeniform. Basidiospores ovoid, ellipsoid to broadly ellipsoid, inamyloid to dextrinoid. Clamp connections present or absent.

Lepiota rubiginosoides Franco-Molano sp. nov.

Lepiotae rubiginosae Pegler, speciei afrinacae, affinis, sed fibulis nullis et basidiosporis minoribus diversa, ulterius a L. rubiginosa cheilocystidiis hyphisque subpileipellis haud incrustatis distans.

Etymology: This species resembles in color L. rubiginosa.

FIGS. 53, 54a-e.

Pileus 1-2 cm diam, convex to plane; surface reddish brown (8E8), entire at the center revealing a reddish brown (8E8) subepicutis toward the margin; white fibrillose scale-like patches on the subepicutis; margin appendiculate. Context up to 2 mm thick, white, changing to pinkish (7A3) when cut. Odor mild. Lamellae free, close, 2 mm broad, white, changing to pale brown with age or when cut; margin entire, not marginate. Stipe 5-7(10) cm long, ± 1.5 mm broad, central, equal; surface, with scattered fibrillose scales, brownish (7C5) at the base, paler at the apex.

Macrochemical tests: positive for tyrosinase throughout basidioma; positive for laccase throughout basidioma; KOH on pileus, negative; NH_4OH on pileus, negative.

Basidiospores (Fig. 54a) 2.7-3.7 x 1.8-2.7 µm ($\overline{Q}$ = 1.58), broadly ellipsoid to ovoid in face view, ellipsoid to broadly ellipsoid in profile, hyaline in KOH, dextrinoid in Melzer's reagent. Basidia (Fig. 54b) narrowly clavate, 4-sterigmata, hyaline, inamyloid, 11.6-16.7 x 3.7-5.5 µm. Pleurocystidia absent. Edge of lamellae heteromorphous with crowded cheilocystidia. Cheilocystidia (Fig. 54c) clavate to cylindric, (16) 20-25 x 3-5 µm, often septate and branched, thin-walled.

Hymenophoral trama formed of hyphae hyaline, inamyloid, 3-6 µm broad, thin-walled, regularly arranged. Subhymenium parenchymatous, 10-15 µm wide; cells 4-12 µm broad. Pileus trama hyaline, inamyloid, composed of slightly interwoven but radially oriented hyphae; hyphae cylindric, septate, 3-7 µm broad. Suprapileipellis (Fig. 54e) formed of three layers. The outermost layer is hymeniform, formed of hyaline, inamyloid, clavate to subpyriform hyphae, septate or not, up to 16 x 6 µm; the middle layer is cellular, ±40 µm thick, with hyaline, inamyloid hyphae, up to 16 µm diam; the inner layer formed of densely interwoven, radially arranged hyphae; hyphae hyaline, inamyloid, cylindric, septate, 3-7 µm broad. Subpileipellis (Fig. 54d) formed of densely interwoven but radially arranged, ±catenulate hyphae; hyphae often branched or anastomosing, hyaline or with reddish to vinaceous pigment, 4-12 µm diam. Stipitipellis parallel and vertically oriented, giving rise to a layer of loosely arranged hyphae; hyphae yellowish in KOH, septate, up to 5 µm broad. Tissue hanging from the margin of pileus formed of interwoven hyphae, hyaline to yellowish in KOH, septate, branched or not, up to 3 µm broad, similar to the inner layer of suprapileipellis. Clamp connections absent.

Material studied: BOLIVIA. DPTO. DE BENI: Prov. Iturralde, N of Rurrenabaque, along Rio Beni, pueblito Capaina, approx. 67°30′W, 14°20′, 5 Apr 1990, Franco-M. 371 (LPB); 10 April 1990, Franco-M. 393 (LPB). COLOMBIA. DPTO. META: Mpio. de San Luis de Cubarral, bosque húmedo a la entrada a San Luis de Cubarral, sobre hoja de palma, Franco-M. 710 (HOLOTYPE, COL); DPTO. MAGDALENA, Parque Nacional Tayrona, camino entre Calabazo y Guachaquita, 10 Jun 1992, Franco-M. 933a (COL).

Distribution: Neotropics, known from Bolivia and Colombia.

Discussion: This species is very close to the African *L. rubiginosa* Pegler, from which it differs in lacking clamp connections and in having smaller basidiospores. In addition, *L. rubiginosa* has mucronate cheilocystidia and the hyphae of the subpileipellis present red incrusted pigments while non-mucronate cheilocystidia and non incrustated hyphae are found in *L. rubiginosoides*.

CHAPTER V

Phenoloxidases Studies

The classification of wood rotting fungi into white- and brown-rot groups is based on the specific ability of fungi to utilize the different components of the wood. It has been shown that only aerobes, primarily wood-decomposing members of Basidiomycetes, metabolize lignin efficiently by production of extracellular phenoloxidases (Kirk, 1985). The activity of these enzymes acting on the components of wood have been studied as a means of identifying fungi lacking distinct morphology and for taxonomic purposes (Niku-Paavola, 1990). Bavendamm (1928) classified wood-rotting fungi into white-rot fungi which produce extracellular phenoloxidase and brown-rot fungi which do not have this ability.

Marr _et_ _al._ (1986) recommended spot testing of the entire radial section of basidiomata for phenoloxidase activity to visualize localization of the enzymes and to obtain semi-quantitative results. He used a point system to score the reaction patterns observed, which converted the reaction area to a numerical 5-point scale (0-4). This scale indicated the extent rather that the intensity of the reaction. Three hundred fifty nine collections representing 222 species of 22 families of Basidiomycetes were examined and grouped into four categories delimited by the quantities of laccase and tyrosinase produced. The four categories were: Group I- Laccase and Tyrosinase absent; Group II- Tyrosinase dominant; Group III- Laccase dominant; and Group IV- Laccase and Tyrosinase reactions equivalent.

The members of Lepiota are saprophytic or terrestrial, non-ectomycorrhizal (Singer, 1986), and are involved in wood degradation (intact wood or wood with certain degree of decomposition). Marr et al. (1986) by testing Leucoagaricus americanus and Leucoagaricus naucinus, classified the Lepiotaceous fungi as a tyrosinase dominant group, however, his sample was not representative of Lepiota s.l.

Marr's et al. (1986) procedure was attempted whenever possible for Lepiota s.l. Syringaldezine was used to test for laccase and p-cresol to test for tyrosinase; reactions were recorded at 5, 15, 30, 60 and 90 minute intervals. Reactions were recorded as positive or negative; if positive the localization of the reaction was specified. In general, a positive reaction appeared within the first 15 minutes; no positive reaction were recorded at times 30 minutes or longer. The test was performed on living fully expanded basidiomata in 14 of the 29 species included in this work. Five tested positive for tyrosinase and eight tested positive for both, one was negative, and none was positive for laccase. In addition, 26 collections of Lepiota s.l. from Bolivia showed that just one tested positive for tyrosinase, while nine were laccase positive, 10 were negative, and six were positive for both.

Results obtained from the Colombian taxa (Table I) indicate that Chlorophyllum, Macrolepiota, Leucoagaricus, and Leucocoprinus belong to Marr's et al. group II (tyrosinase dominant group) while Rugosospora and Lepiota s.s. belong to group IV (laccase and tyrosinase reactions are about equal). The Bolivian taxa however put Leucoagaricus, Leucocoprinus and Lepiota s.s. in group III (laccase dominant group). Considering that spot test reagents, syringaldezine and p-cresol, were effective for detection of phenoloxidases, the lack of consistency in the results within the group indicates that phenoloxidases are widespread along the members of Lepiota s.l. and that the production of the enzymes is an ecological response rather than locating sites of active growth (Marr, 1986). Thus, it is neccesary to test the same taxa under different ecological conditions, and to use a larger sample size representing different genera before presence or absence of phenoloxidases can be used as useful character at any taxonomic level.

CHAPTER VI

Phylogenetic Comments

Lepiota s.l. belongs to the Agaricaceae together with Agaricus; it differs from the latter in having white rather than brown basidiospores. According to Kühner (1980), due to the lack of paleontological documentation, it is not possible to reconstruct a phylogenetic tree of the Hymenomycetes. However, based on morphological characters, the phylogenetic relationship of some groups have been studied (Baroni, 1981; Homola, 1975; Vilgalys, 1986). Although the real number of species belonging to generic segregates of Lepiota s.l. is not known, and no phylogentic studies of these segregates have been done, it is certain that primitive and derived characters are found in each genus.

The major characters distinguishing the genera within Lepiota s.l. are the features of the basidiospores and the pileipellis; other characters are important at the specific level. The following features are to be considered in any analysis of generic relationships. Unless otherwise cited the information was taken from Kühner (1980).

Basidiomata. In boletes, species with large basidiomata seem to be more derived than species with small basidiomata (Thiers, 1971). In Lepiota s.l., Chlorophyllum and Macrolepiota are characterized by having the largest basidiomata within the group.

Pileus. According to Bas (1969) in Amanita section Lepidella an entire pileus margin is more primitive than a sulcate one. Leucocoprinus, Hiatulopsis and some species of Leucoagricus have a pectinate to sulcate margins.

Pileipellis. The cutis-type of pileipellis is considered more primitive than a trichodermium or hymenodermium (Homola, 1975); the epithelial-type is the more derived one (Kühner, 1980). The cutis-type is typical of most species of Leucoagaricus and of sections Ovisporae and Anomalae of Lepiota s.s. An epithelial-type is found in Cystolepiota, Januaria, and some species of Leucocoprinus.

Basidiospores. Characters of the basidiospores such as a differentiated endosporium, apical differentiations (a germ pore), and thick-walls are derived characters (Kühner, 1980). These characters are present in Clarkeinda, Chlorophyllum, Macrolepiota, Volvolepiota, some species of Leucococoprinus, and some species of Leucoagaricus.

The presence of wall ornamentation is considered a derived character. Although only three genera, Hiatulopsis, Smithiomyces, and Rugosospora are characterized by having ornamented basidiospores, some species in Lepiota s.s. and Leucoagaricus have basidiospore ornamentation.

Kühner (1980) considered that basidiospores possessing one nucleus are more primitive than those with two nuclei. Furthermore, he (1980) pointed out that chromosporic basidiospores are more derived than leucosporic basidiospores. Chromosporic basidiospores are typically binucleate. Excepting Chlorophyllum and Clarkeinda, with green basidiospores, the basidiospores of Lepiota s.l. are characterized by being leucosporic. However, with the exception of Cystolepiota and section Anomalae of Lepiota s.s, the basidiospores of Lepiota s.l. are binucleate.

Globose basidiospores are more primitive than ellipsoid basidiospores (Bas, 1969). Globose basidiospores are found only in Hiatulopsis; the basidiospores of the other genera range from ovoid, ellipsoid, to fusoid. In two sections of Lepiota s.s the basidiospores are spurred.

Lamellae. Free lamellae are considered a derived character. The presence of free lamellae is one of the diagnostic features of Lepiota s.l.

Hymenium. The presence of pseudoparaphyses is considered a derived character. Pseudoparaphyses are well developed only in some species of Leucocoprinus.

Subhymenium. The cellular subhymenium that characterize species of Lepiota s.l. is a derived character (Kühner, 1980).

Cystidia. The presence of cystidia is considered a derived character. Hiatulopsis is the only genus without cystidia (cheilo- or pleurocystidia).

Clamp connections. The presence of clamp connections is considered a primitive character. Clamp connections are lacking in Leucocoprinus, most species of Leucoagaricus, and in the species belonging to section Anomalae of Lepiota s.s.

Stipe. Centrally stipitate basidiocarps are considered to be more primitive, and eccentrically stipitate basidiocarps more derived (Baroni, 1981). All the species of Lepiota s.l. have centrally stipitate basidiomata.

Annulus. The presence of an annulus, which is one of the diagnostic features of Lepiota s.l.; is considered to be a derived character.

general, the genera belonging to Lepiota s.l. have a combination of primitive and derived characters. However, I agree with Heinemann (1973a) that the genera belonging to the tribe Leucocoprineae form the group of the most derived Lepiotas; within this group the genus Leucocoprinus seems to be the most derived because it has the highest number of these putatively derived characters. Leucoagaricus is probably intermediate between Leucocoprinus and Macrolepiota as pointed out by Singer (1986).

Cladistic analysis.

Cladistic analysis is a systematic method that attempts to summarize knowledge about the similarities among organisms in terms of branching diagrams, called a cladogram (Cracraft, 1983). Although criticized (Cronquist, 1987), the cladistic theory proposed by Hennig (1966) attempts to reconstruct the evolutionary history of a group using empirical methods, emphasizing shared derived characters (synapomorphies).

A cladistic analysis to understand the phylogenetic relationships of the genera of <u>Lepiota</u> s.l. was attempted. The technique assumed that the taxa under study are monophyletic (that is, descendend from a common ancestor).

This study was carried out with compatible versions of MacClade 2.97 and PAUP 3.0 which allow the use of polymorphic characters. Hennig 86 version 1.5 and Phylip version 3.4 were also tried. Multistate characters were unordered. Outgroup comparison was used to polarize characters.

The cladistic analysis of the genera belonging to <u>Lepiota</u> s.l. using the set of characters and the data matrix in Table II and III, was performed to evaluate the relationships between genera and to test that either <u>Agaricus</u> or <u>Amanita</u> is the sister group of <u>Lepiota</u> s.l. Since some authors (Kühner, 1980; Singer, 1986) consider <u>Agaricus</u> to be very close to <u>Lepiota</u>, the analysis was also performed without <u>Amanita</u>.

Although several attempts were performed, including the elimination of taxa and/or characters, the results consistently supported Singer (1986) showing a close relationship between <u>Chlorophyllum</u> and <u>Clarkeinda</u>; both are characterized by having green basidiospores. The grouping of the other genera was not constant and in several cases resolution of genera was not obtained. In some cases, Agaricus was in the ingroup and in others it was significantly isolated from the rest of the clade. Amanita shows several autapomorphous characters that are considered to be the end point of a character transformation (Cracraft, 1983), such characters are only good for characterization of the taxon and not useful in a cladistic analysis (Wiley et al., 1991; Forey et al. 1992).

After several attempts, I have come to the conclusion that additional data and different interpretations of the character states will have to be considered before an informative cladistic analysis can be developed for Lepiota s.l. It is premature to do a cladistic analysis at the generic level at this time. Cladistic analyses are done only on genera for which there is some evidence of monophyly, and, while it is true that there are characters by which some of the smaller genera can be identified, there is no evidence that these characters are really synapomorphic. This evidence can only be obtained by including all the species of the largest genera (Lepiota, Leucocoprinus, and Leucoagaricus) in an analysis. Furthermore, analysis to provide sister-group relationships is not possible if monographs of the largest genera are lacking.

In this study I recognize several generic segregates, and the strongest support for the recognition of these segregates would come from cladistic analysis. However, for Lepiota s.l. cladistic analysis is an inappropiate method at this time. Cladistic analyses depend on having monophyletic groups and I do not have evidence that any monophyletic groups exist solely within the Colombian mycota. Thus, I am using the information gathered from this study to start a data set to be used in a future cladistic analysis, but that analysis, by necessity, will have to wait until a monograph of Lepiota sensu lato is completed.

SUMMARY

1. A preliminary taxonomic treatment of the species of Lepiota s.s. and related species that occur in Colombia is presented.

2. The limits of the genera belonging to Lepiota s.l. used in this work are essentially those of Singer (1986). Singer placed the genus in the family Agaricaceae and divided the family into four tribes: Leucocoprineae and Lepioteae which include the genera of Lepiota s.l., Agariceae whose species possesses brown basidiospores, and Cystodermateae that is best placed in the Tricholomataceae. In this work the genus Rugosospora has been added to Singer's tribe Leucocoprineae.

3. The tribe Leucocoprineae is characterized by having basidiospores with or without germ pore and with metachromatic endosporium. Representatives in Colombia include one species of Chlorophyllum, two species of Macrolepiota, five species of Leucoagaricus, five species of Leucocoprinus, and one species of Rugosospora.

4. The tribe Lepioteae is characterized by having basidiospores without germ pore and with non-metachromatic endosporium. Representatives in Colombia include one

species of Cystolepiota and fourteen species of Lepiota s.s.

5. The genus Lepiota s.s. is represented in Colombia by the sections Stenosporae, Lepiota, Ovisporae, and Anomalae of Singer's classification. Section Lilaceae (Bon, 1981) was included in this work to accomodate a species having hymeniform pileipellis, and ellipsoid and inamyloid basidiospores.

6. Macrolepiota colombiana, M. quindiana, Leucoagaricus incrustatus, L. zarzalensis, L. guachacanus, Cystolepiota coquisorum, Lepiota bisporigera, L. theobromicola, L. narinyensis, L. papillata, L. sulphureocyanescens, L. belmirensis, and L. rubiginosoides are described for the first time and one new combination Leucocoprinus zamurensis is proposed.

7. Results of phenoloxidase tests performed in fresh basidiomata of fourteen of the 29 species included in this work indicate that the species of Chlorophyllum, Macrolepiota, Leucoagaricus, and Leucocoprinus belong to Marr et al. group II (tyrosinase dominant group), while Rugosospora and Lepiota belong to group IV (laccase and tyrosynase reactions are about equal).

8. Although the strongest support for the recognition of the generic segregates of Lepiota s.l. would come from a cladistic analysis, this is an inappropiate method at this time. Cladistic analyses depend on having monophyletic groups and there is no evidence that any monophylectic group exists solely in Colombia.

9. Based on the assumption that common characters are primitive and that uncommon characters are derived, I agree with Heinemann (1973a) that the genera belonging to the tribe Leucocoprineae form the group of the most derived Lepiotas. Within this group the genus Leucocoprinus seems to be the most derived because it has the highest number of these putatively derived characters. Leucoagaricus is probably intermediate between Leucocoprinus and Macrolepiota as pointed out by Singer (1986).

TABLE I. Result of Spot Tests for **Laccase** and **Tyrosinase** activity in basidiomata of _Lepiota_ s.l.

Specific Epithet	Tyrosinase	Laccase	Genus
molybdites	+	-	_Chlorophyllum_
colombiana	+	-	_Macrolepiota_
hortensis	+	-	_Leucoagaricus_
rubrotinctus	+	-	_Leucoagaricus_
zarzalensis	+	-	_Leucoagaricus_
zamurensis	+	+	_Leucocoprinus_
tenellus	+	-	_Leucocoprinus_
cepaestipes	+	+	_Leucocoprinus_
pseudorubiginosa	+	+	_Rugosospora_
theobromicola	+	+	_Lepiota_
azalearum	+	+	_Lepiota_
belmirensis	+	+	_Lepiota_
guatopoensis	-	-	_Lepiota_
rubiginosoides	+	+	_Lepiota_

TABLE II. Characters used in the cladistic analyses of _Lepiota_ s.l.

	Transformation series				
Characters	0	1	2	3	4
1. Spore print	White	Green	Brown		
2. Germ pore	Absent	Present			
3. Spore wall in Melzer's	Inamyloid	Amyloid	Dextrinoid		
4. Spore wall in Cresyl blue	Not metachromatic	Metachromatic			
5. Spore wall ornamentation	Smooth	Ornamented			
6. Spore wall thickness	Thin	Thick			
7. Clamp connections	Present	Absent			
8. Volva	Absent	Present			
9. Habit	Saprophytic	Mycorrhizal			
10. Hymenophoral trama	Regular	Bilateral			
11. Gelatinization	Absent	Present			
12. Acrophysalydes	Absent	Present			
13. Margin of pileus	Smooth	Pectinate			
14. Sphaerocysts	Absent	Present			
15. Subhymenium	Ramose	Cellular			
16. Pseudoparaphyses	Absent	Present			
17. Spore Shape	Globose	Ovoid	Ellipsoid	Fusoid	Spurred
18. Pileipellis	Cutis	Hymenodermium	Trichodermium	Epithelium	

TABLE III. Data matrix for Lepiota s.l.

	Transformation series																	
Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
1	0	0	0 1	0	0	0	0 1	1	1	1	1	1	0 1	0	0	0	0	0
2	2	0 1	0	0	0	0	0 1	0	0	0	0	0	0	0	1	0	1	1
3	1	1	2	1	0	1	1	1	0	0	0	0	0	0	1	0	1	1
4	1	1	2	1	0	1	1	0	0	0	0	0	0	0	1	0	1	1
5	0	1	2	1	0	0	0	1	0	0	0	0	0	0	1	0	1	1 0
6	0	1	2	1	0	0 1	0	0 1	0 1	0	0	0	0	0	1	0	1	1 2
7	0	0 1	2	1	0	0 1	1	0	0	0	0 1	0	0 1	0	1	1	2	1 2
8	0	1	2	1	0	0 1	1	0	0	0	0	0	1	0 1	1	0	1	2 3
9	0	0	2	1	1	0	0	0	0	0	0	0	0	0	1	0	2	1
10	0	0	2	1	0	0	1	0	0	0	1	0	1	0	1	0	2	0
11	0	0	0	0	1	0	0	1	0	0	0	0	0	1	1	0	2	2
12	0	0	0	1	1	0	0	0	0	0	0	0	1	0	1	0	0	2
13	0	0	2	0	1	0	1	0	0	0	0	0	1	0	1	0	2	2
14	0	0	2	0	0	0	0	0	0	0	0	0	0	1	1	0	3	2
15	0	0	2	0	0	0	0	0	0	0	0	0	0	0	1	0	3	2
16	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	3	2
17	0	0	2	0	0	0	0	0	0	0	0	0	0	1	1	0	4	1
18	0	0	2	0	0 1	0	0	0	0	0	0	0	0	1	1	0	4	2
19	0	0	2	0	0	0	0	0	0	0	0	0	0	1	1	0	3	2
20	0	0	2	0	0	0	0	0	0	0	0	0	0	1	1	0	2	2
21	0	0	2	0	0	0	1	0	0	0	0	0	0	1	1	0	2	2
22	0	0	1	0	0	0	1	0	0	0	0	0	0	1	1	0	2	2
23	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	2	1
24	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	2	1

Taxa. 1. Amanita; 2. Agaricus; 3. Clarkeinda; 4. Chlorophyllum; 5. Volvolepiota; 6. Macrolepiota; 7. Leucoagaricus; 8. Leucocoprinus; 9. Rugosospora; 10. Sericeomyces; 11. Smithiomyces; 12. Hiatulopsis; 13. Januaria; 14. Cystolepiota; 15. Lepiota Sect. Echinatae; 16. L. Sect. Amyloidae; 17. L. Sect. Cristatae; 18. L. Sect. Stenosporae; 19. L. Sect. Lepiota; 20. L. Sect. Ovisporae; 21. L. Sect. Anomalae; 22. L. Sect. Amylosporae; 23. L. Sect. Lilaceae; 24. Chamaemyces.

FIG. 1. Colombian map showing the four topographic regions. 1. Pacific Coast (Chocó). 2. Atlantic Coast. 3. Andean region. 4. Eastern lowlands. The circles indicate the Departments where collecting was carried out.

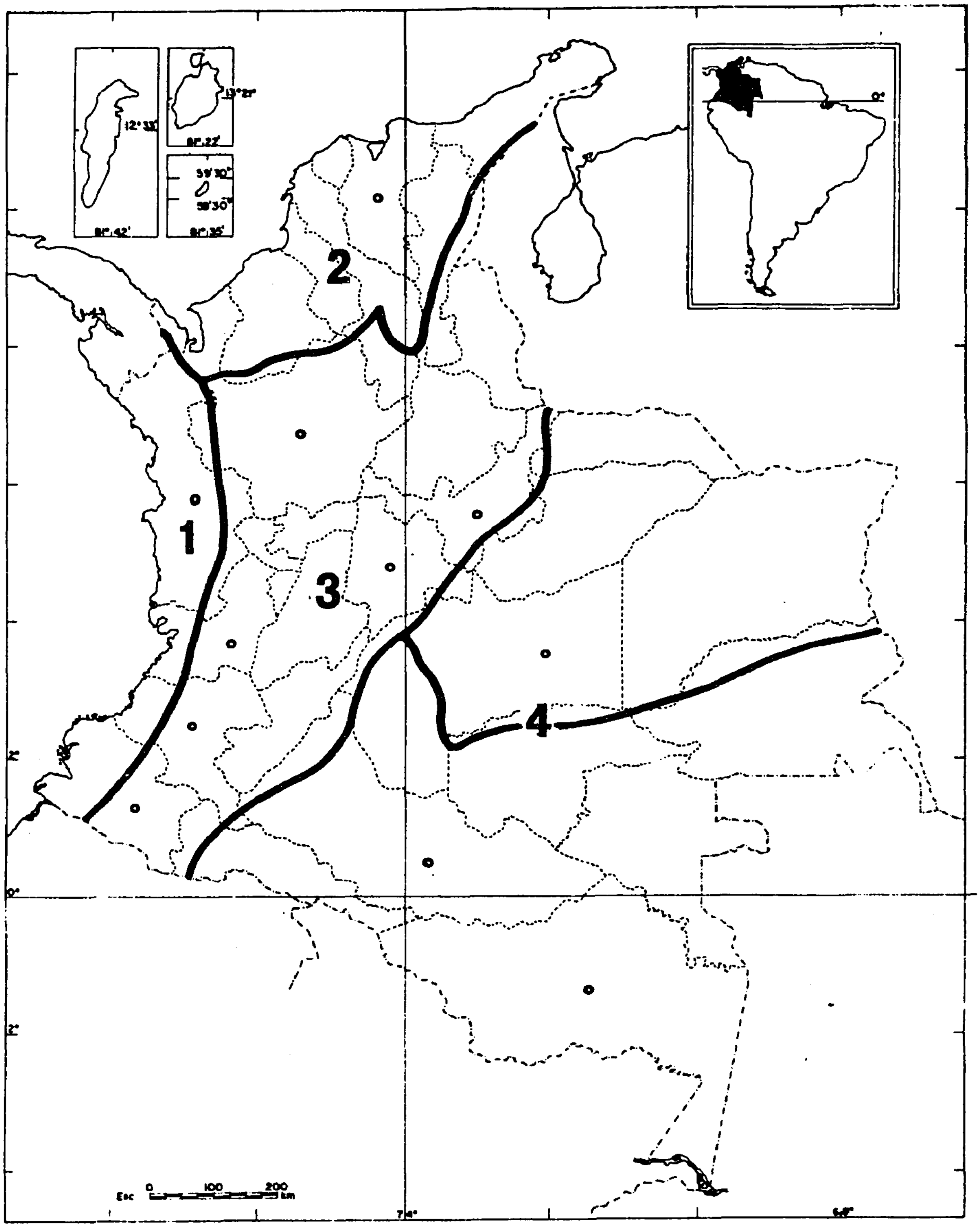
12°33'
13°21'
81°22'
81°42'
81°35'
0°
2
1
3
4
2°
Esc 0 100 200 km
74°
68°

FIG. 2. Germ pores. a. Metachromatic endosporium and non-metachromatic medulla, (ap) apiculus, (cp) cytoplasm, (nm) non-metachromatic medulla, (gp) germ pore, (me) metachromatic endosporium, (sw) spore wall, medulla. b. Metachromatic endosporium and (mm) metachromatic medulla. c. Broad germ pore but medulla is not present. d. Pore formed by thinness of the wall at the apex of basidiospore, (gp) germ pore.

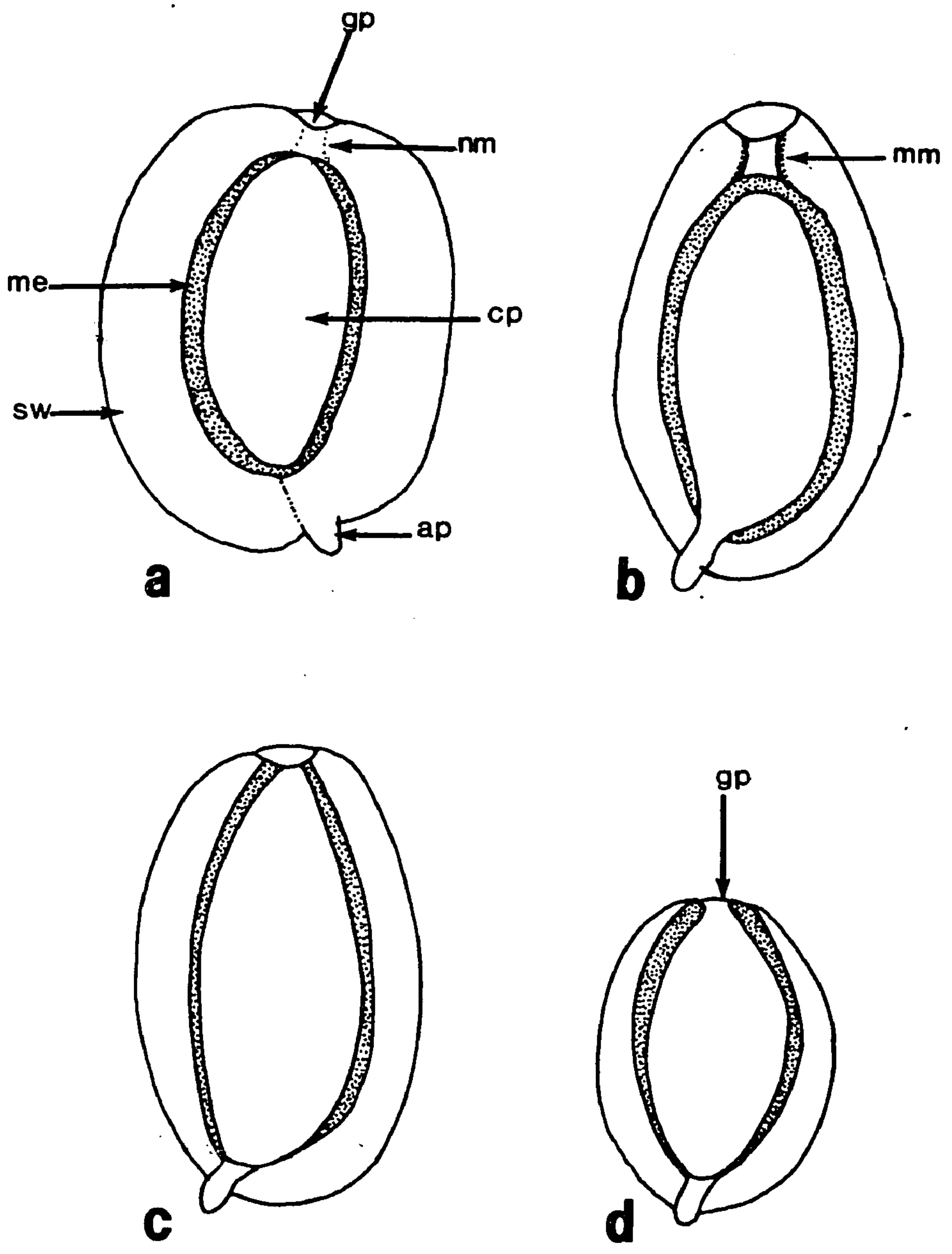
gp
nm
mm
me
cp
sw
ap
a
b
gp
c
d

FIG. 3. Annulus. a. Free edge. b. Inner side. c. Outer side. d. Attached edge.

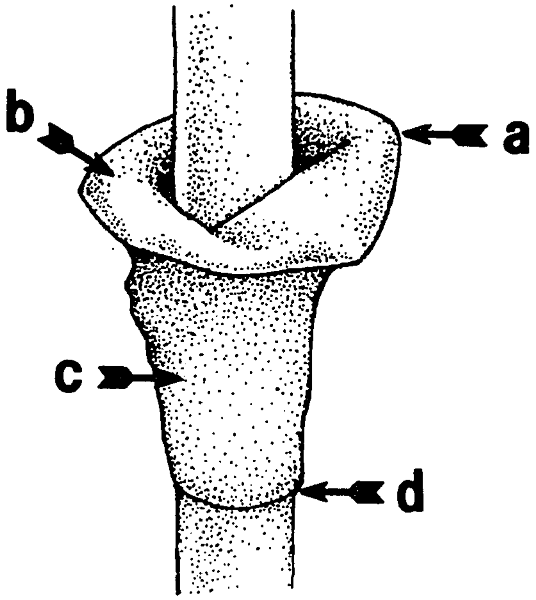
b
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FIG. 4. *Chlorophyllum molybdites* (*Halling 4499*). Habit (±1/2X).

FIGS. 5a-e. Line drawings of the microscopic features of *Chlorophyllum molybdites* (*Franco-M. 892*). a. Basidiospores. b. Basidia. c. Cheilocystidia. d. Pileipellis. e. Trama of pileus. Scale lines = 10 µm.

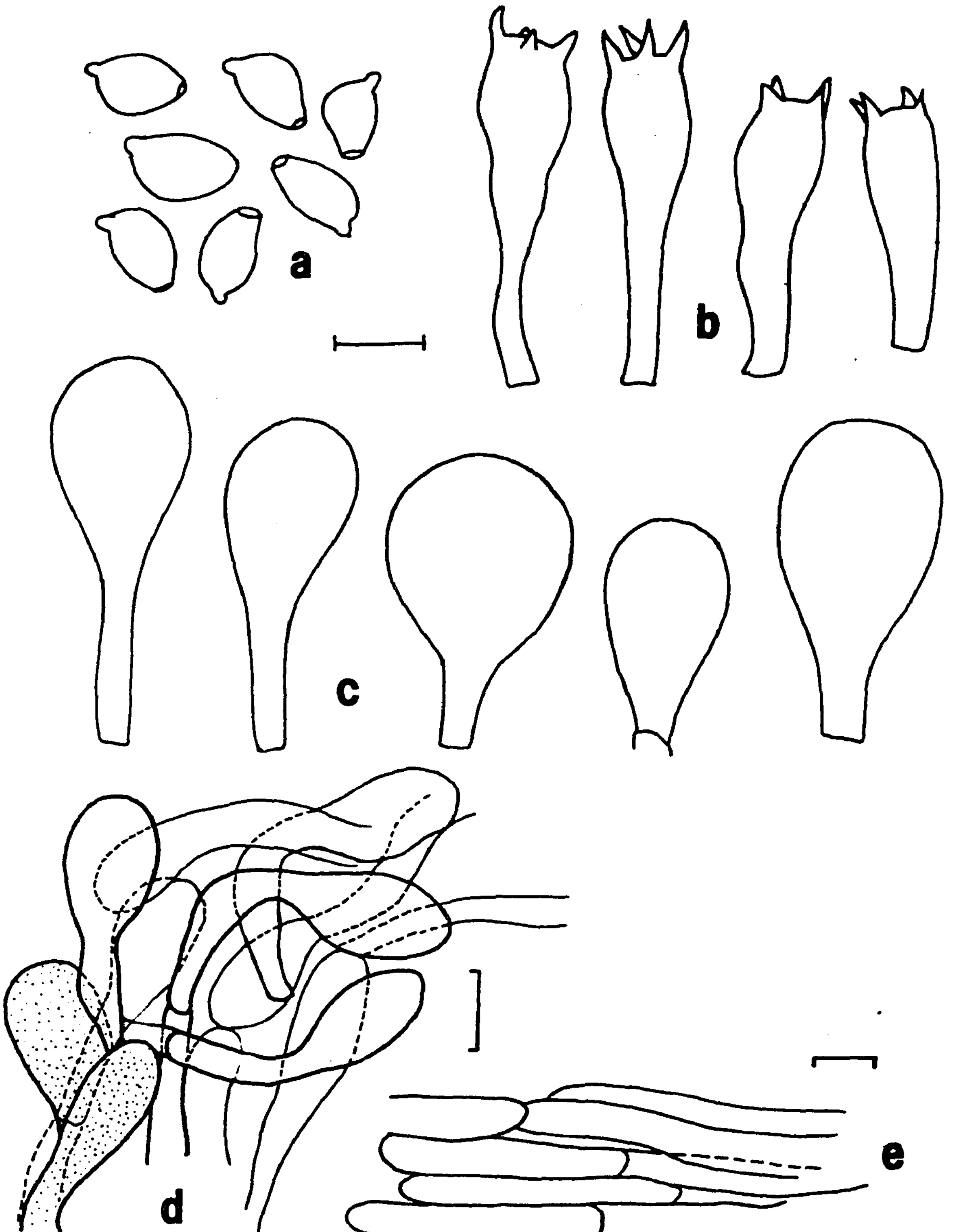
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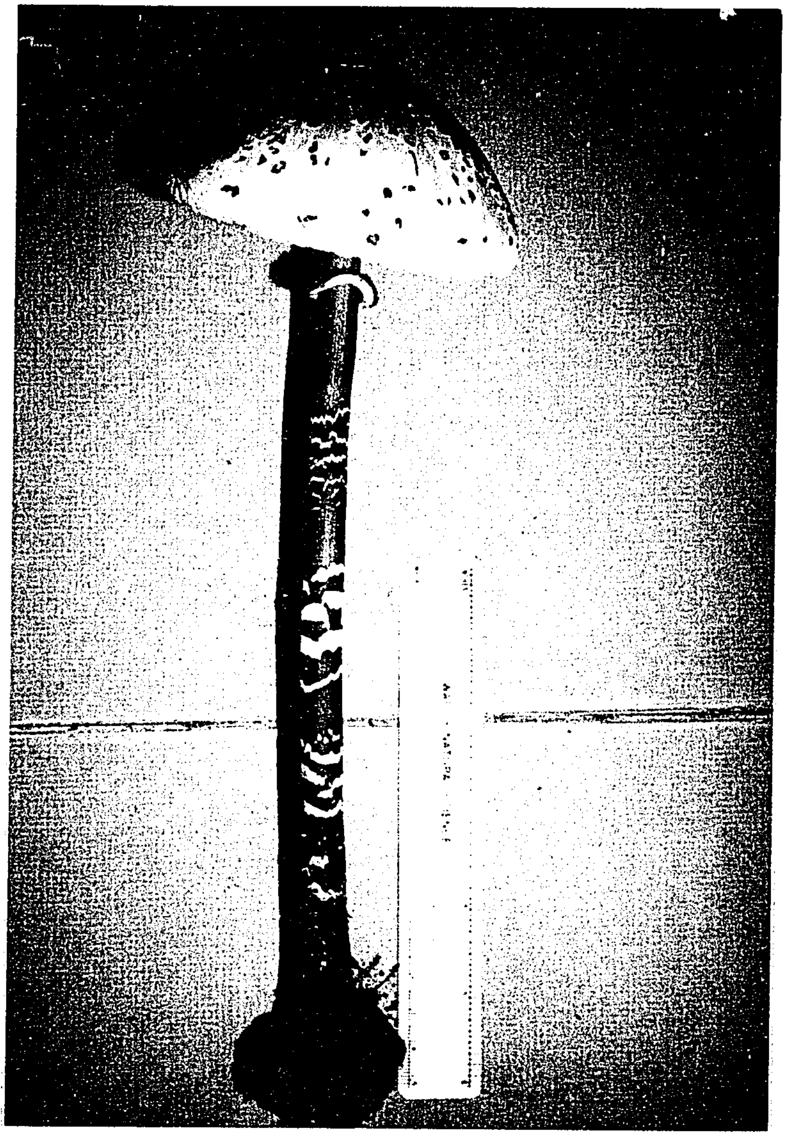
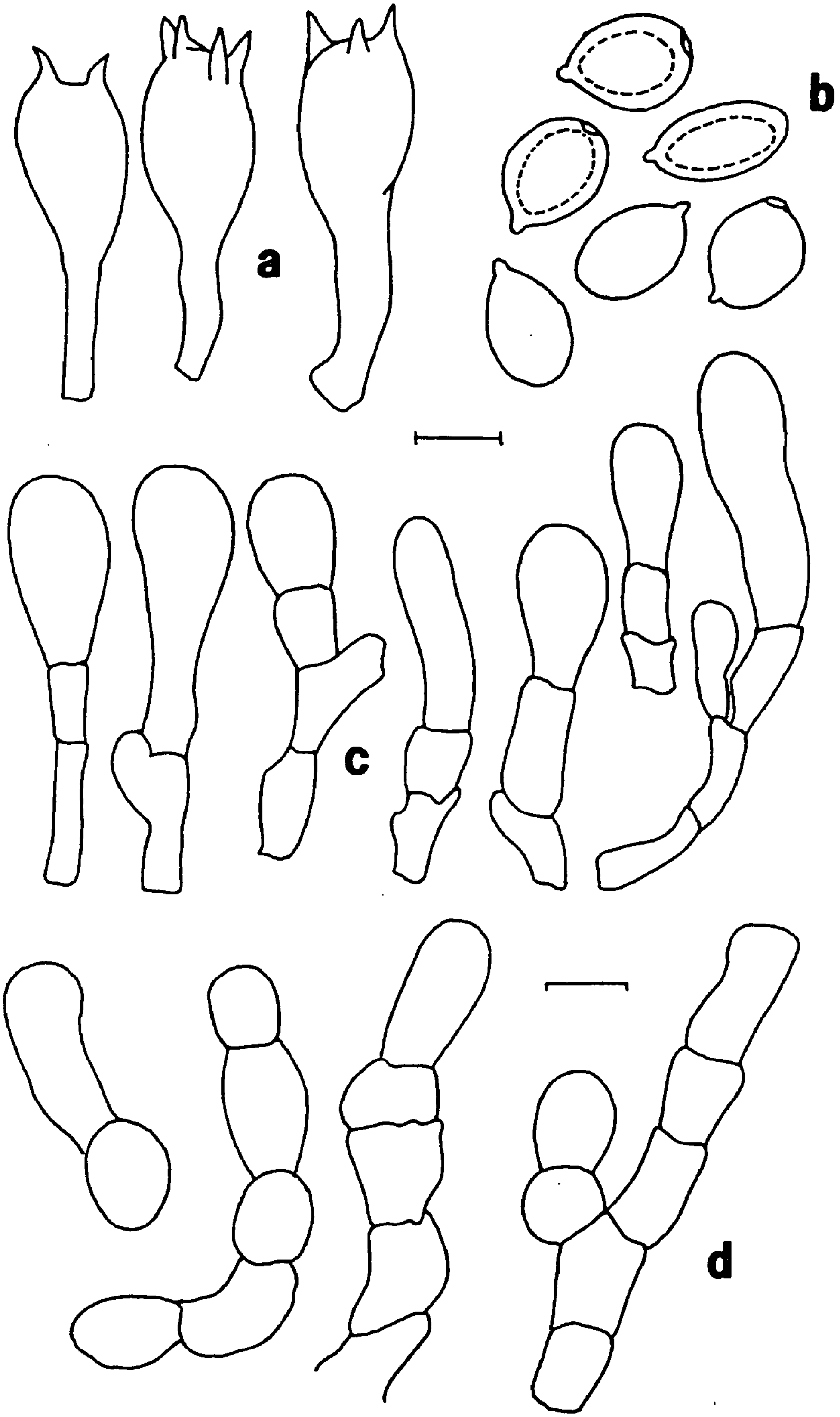
FIG. 6. *Macrolepiota colombiana* (*Franco-M. 775*). Habit (±1/2X).



FIGS. 7a-d. Line drawings of the microscopic features of Macrolepiota colombiana (Franco-M. 775). a. Basidia. b. Basidiospores. c. Cheilocystidia. d. Pileipellis elements. Scale lines = 10 μm.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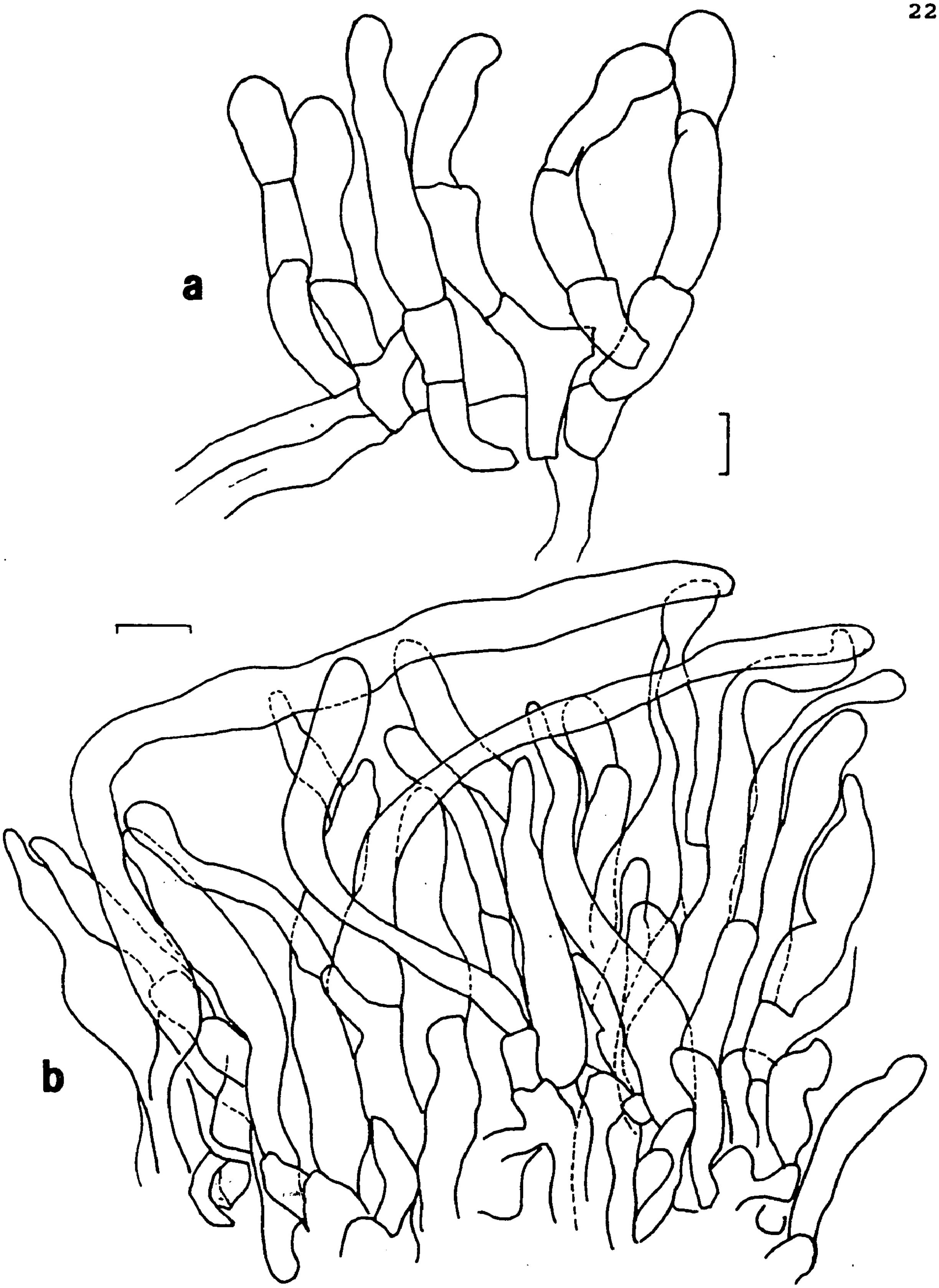
FIGS. 8a-b. Line drawings of the suprapileipellis: a. *Macrolepiota colombiana* (*Franco-M. 775*). b. *Macrolepiota procera* (*Franco-M. 539*). Scales lines = 10 µm.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FIGS. 9a-f. Line drawings of the microscopic features of Macrolepiota quindiana (A. Peñuela and R. Bernal 328). a. Basidiospores. b. Basidia. c. Cheilocystidia. d. Suprapileipellis. e. Subpileipellis. f. Annulus. Scale lines = 10 μm.

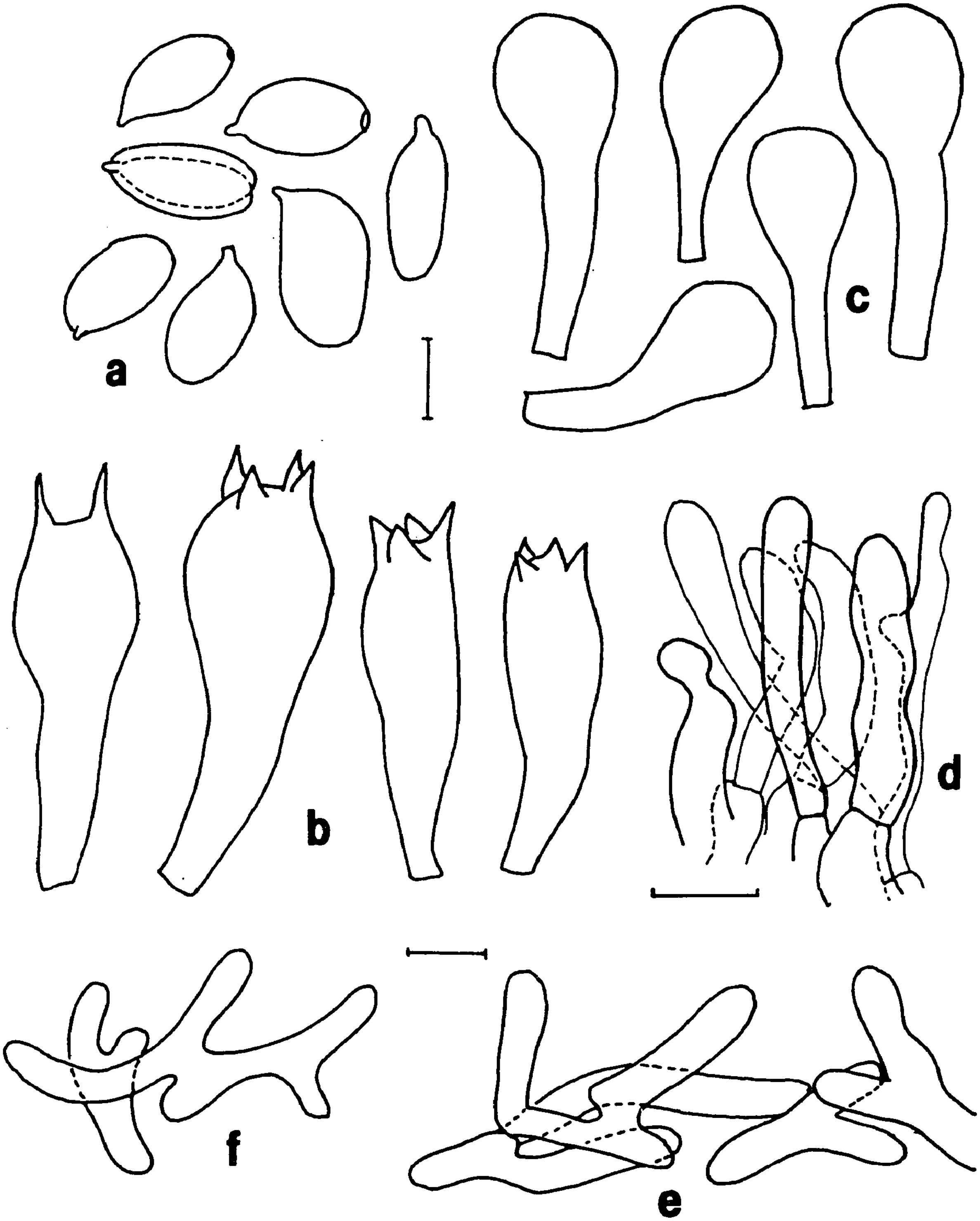
a
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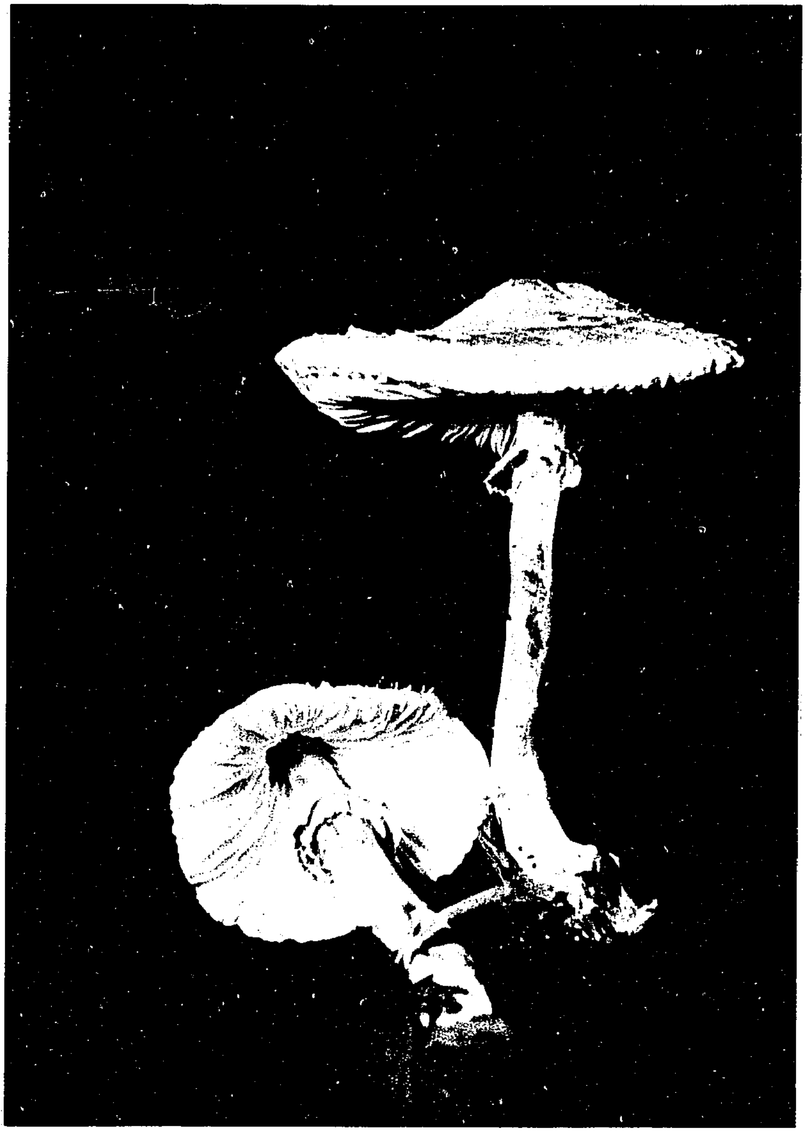
FIG. 10. *Leucoagaricus hortensis* (*Franco-M. 575*). Habit (±1X).



FIGS. 11a-d. Line drawings of the microscopic features of Leucoagaricus hortensis (Franco-M. 575). a. Basidiospores. b. Basidia. c. Cheilocystidia. d. Suprapileipellis elements. Scale lines = 10 μm.

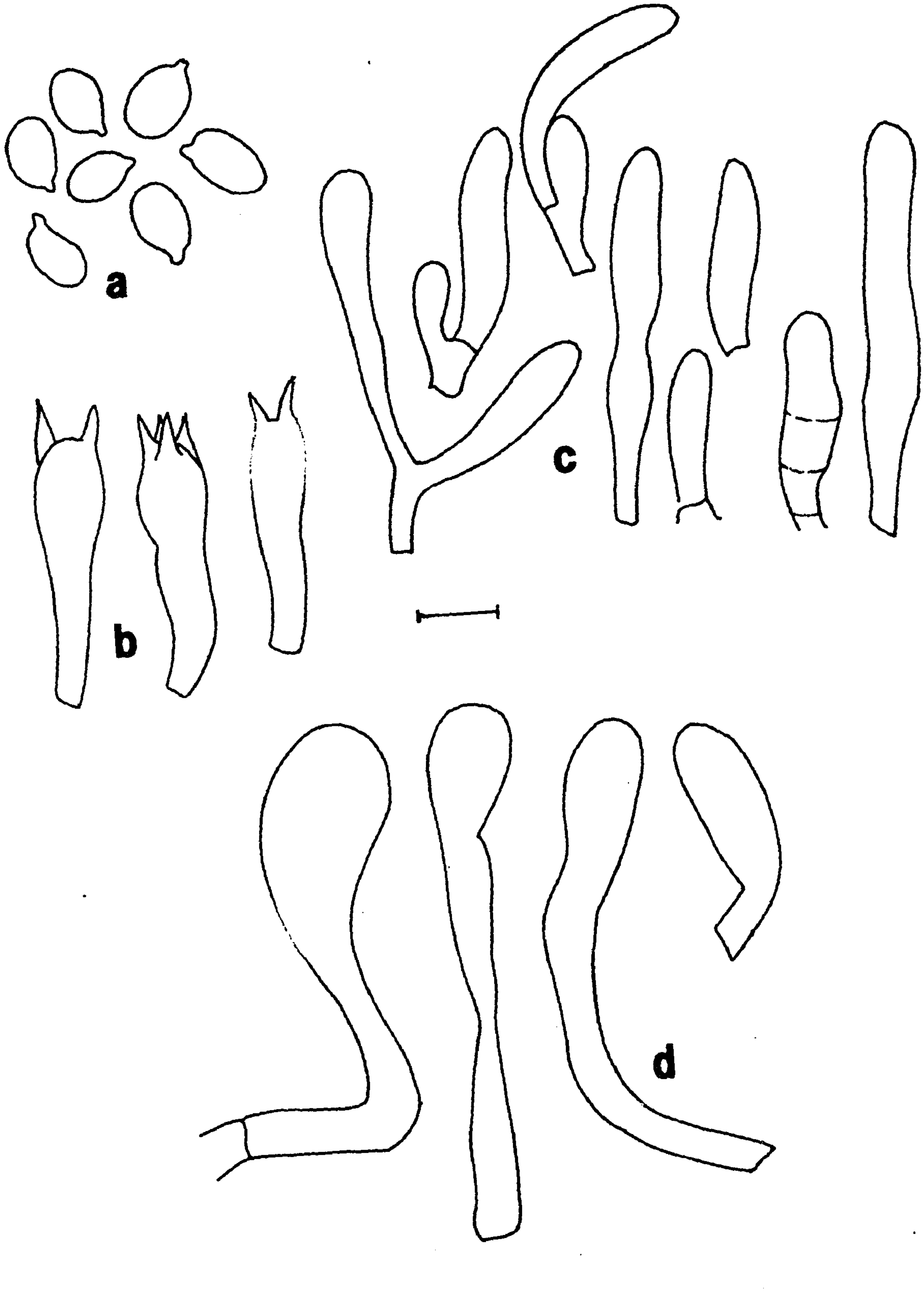

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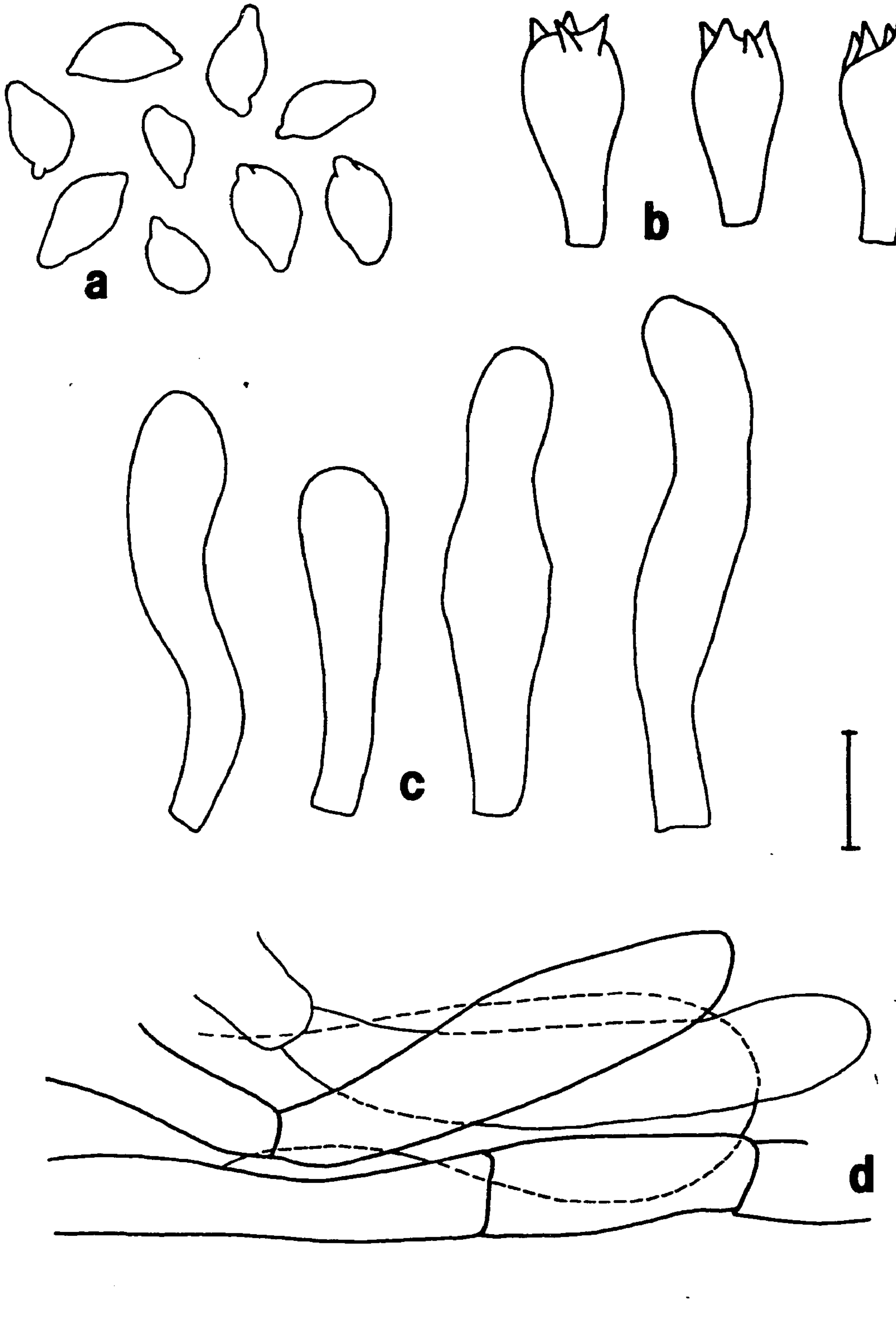
FIG. 12. *Leucoagaricus* *rubrotinctus* (*Franco-M. 886*). Habit (±1/2X)

FIGS. 13a-d. Line drawings of the microscopic features of *Leucoagaricus rubrotinctus* (*Franco-M. 886*). a. Basidiospores. b. Basidia. c. Cheilocystidia. d. Pileipellis elements. Scale lines = 10 μm.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FIGS. 14a-d. Line drawings of the microscopic features of Leucoagaricus incrustatus (Franco-M. 124). a. Basidiospores. b. Basidia. c. Cheilocystidia and pleurocystidia as observed in Melzer's reagent. d. Cheilocystidia and pleurocystidia in KOH. Scale lines = 10 μm.

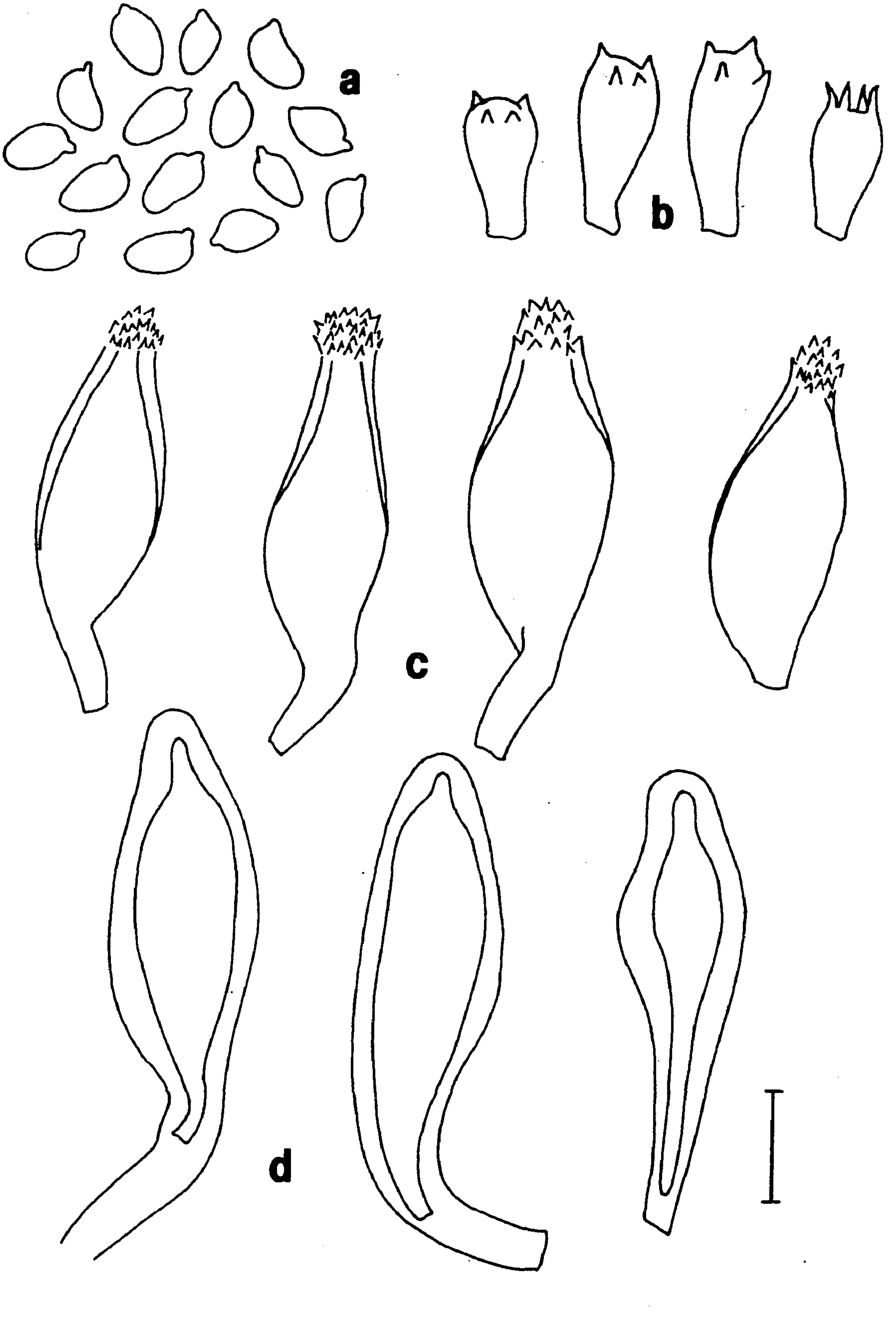
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FIG. 15. *Leucoagaricus zarzalensis* (*Franco-M. 409*). **Habit** (±1/2X).

FIGS. 16a-d. Line drawings of the microscopic features of *Leucoagaricus zarzalensis* (*Franco-M. 409*). a. Basidiospores. b. Basidia. c. Cheilocystidia. d. Pileipellis elements. Scale lines = 10 µm.

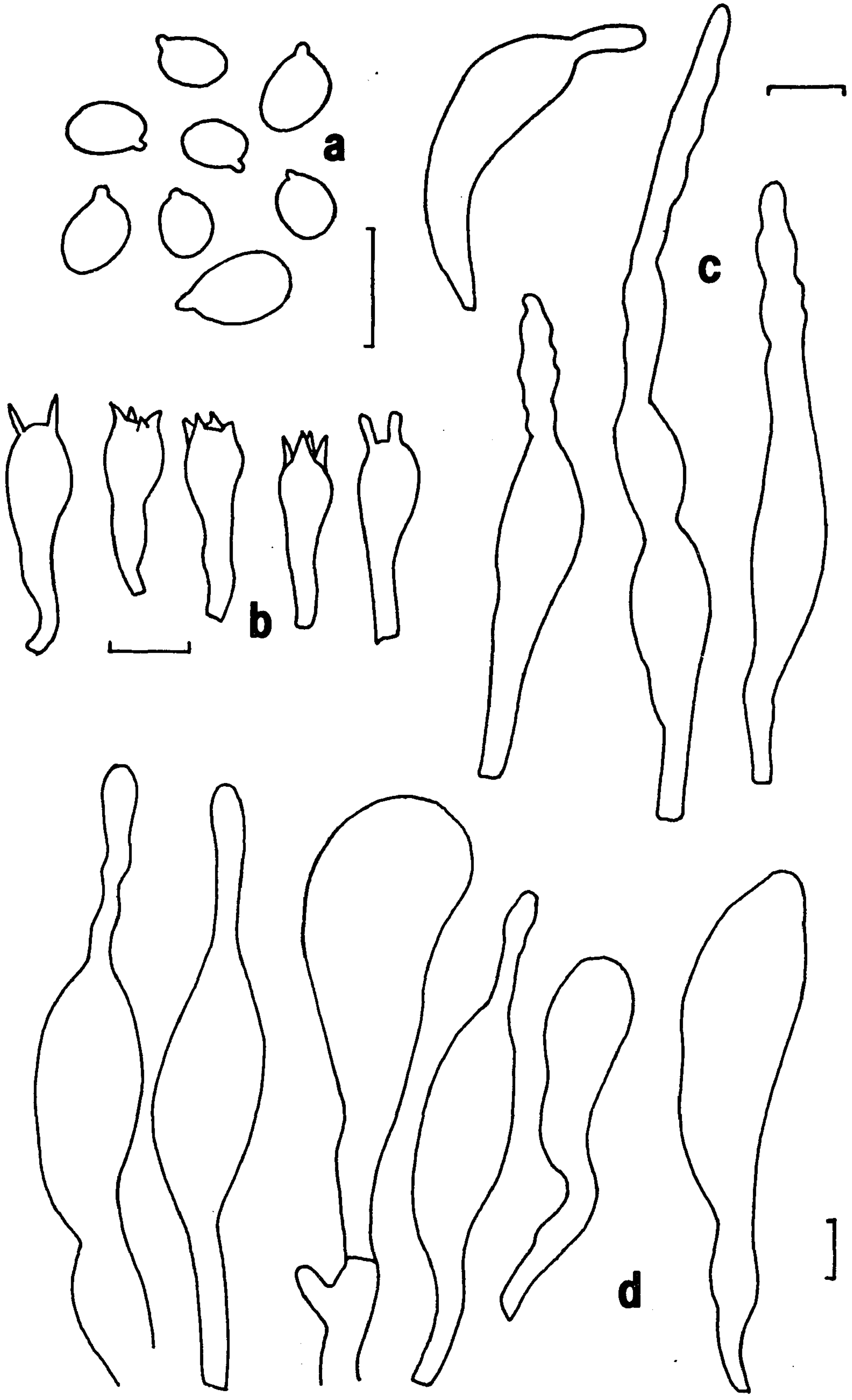
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FIG. 17a-d. Line drawings of the microscopic features of *Leucoagaricus guachacanus* (*Franco-M. 961*). a. Basidiospores. b. Basidia. c. Cheilocystidia. d. Pileipellis. Scale lines = 10 μm.

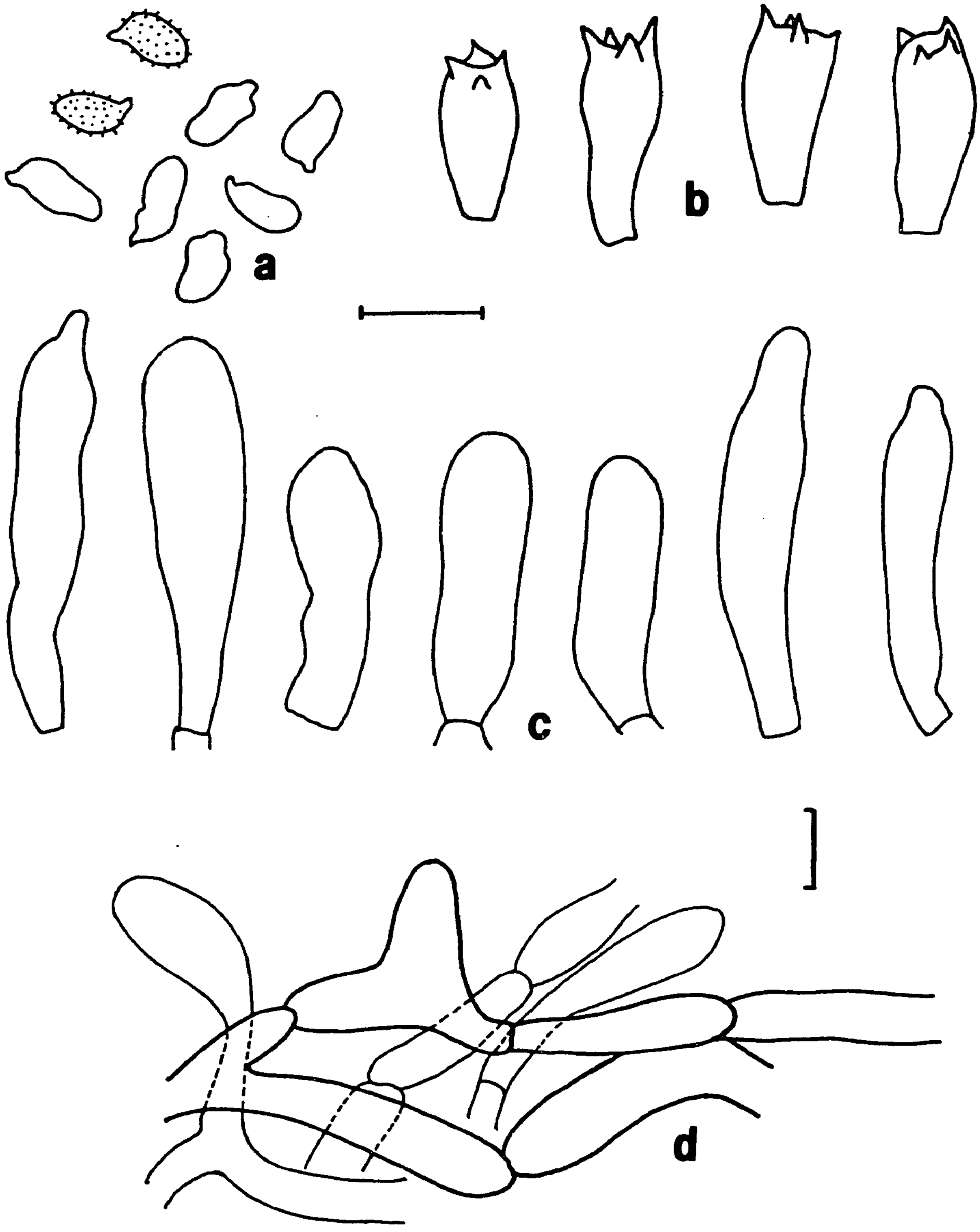
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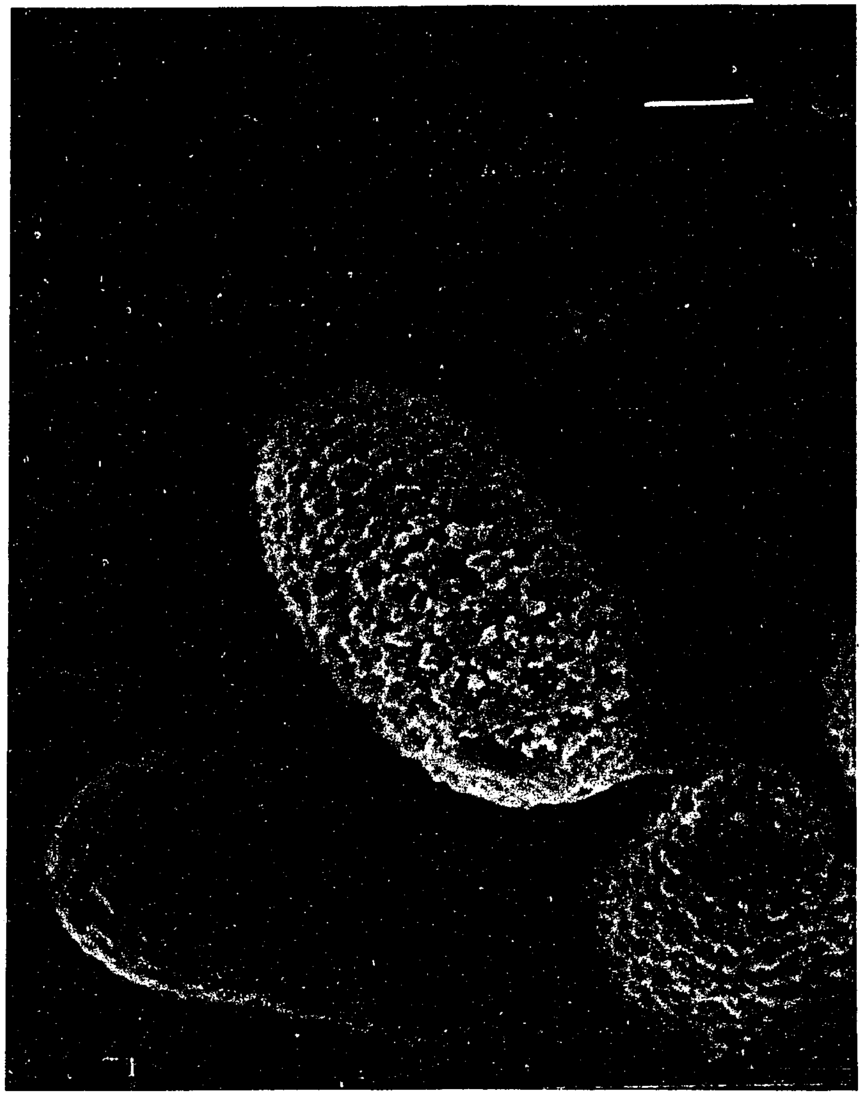
FIG. 18. Leucoagaricus guachacanus (Franco-M. 961). SEM microphotography of basidiospores. Scale line = 1 μm.


1

FIGS. 19a-e. Line drawings of the microscopic features of *Leucocoprinus zamurensis* (Franco-M. 857). a. Basidiospores. b. Basidia. c. Cheilocystidia. d. Pleurocystidia. e. Suprapileipellis. Scale lines = 10 μm.

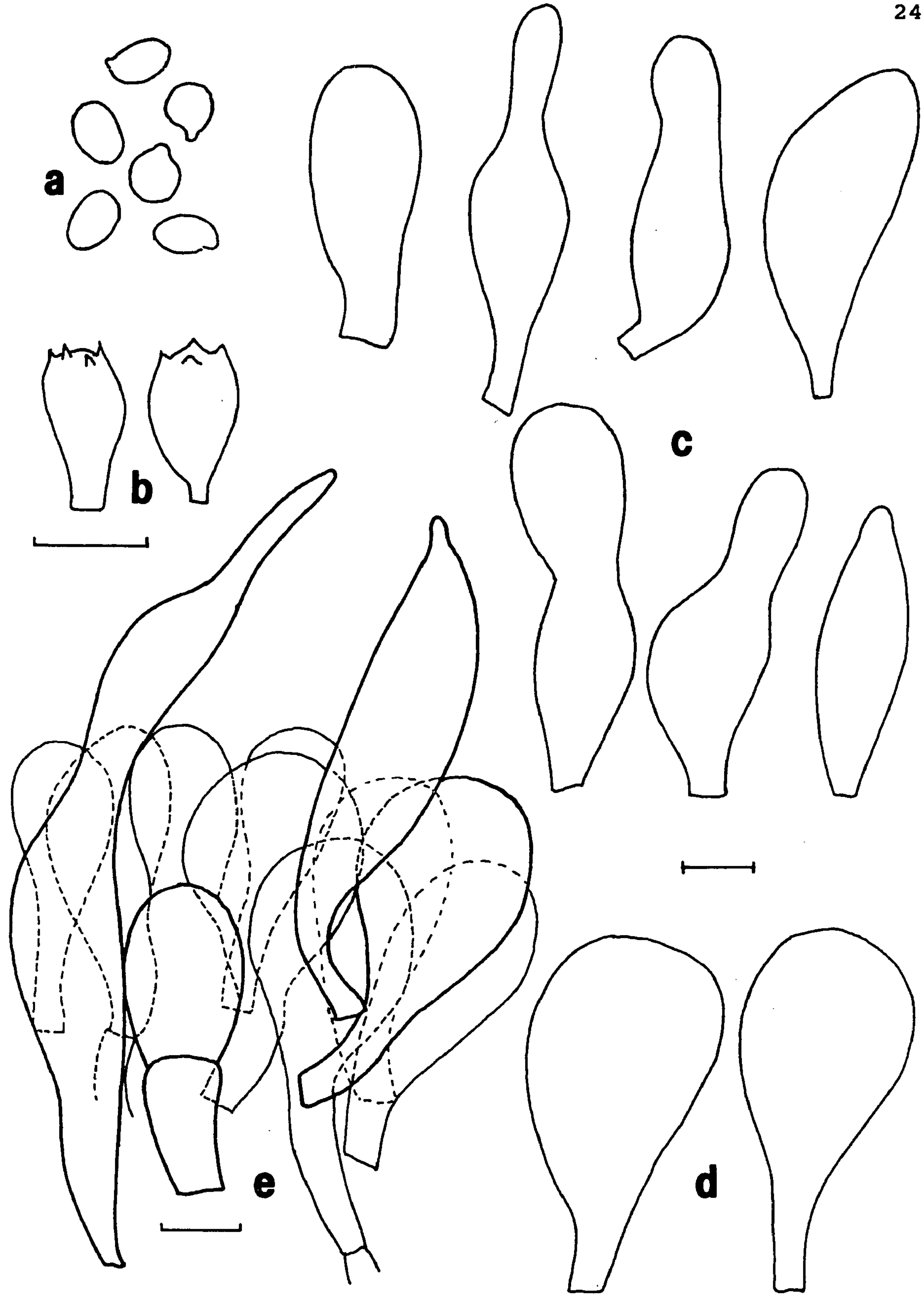

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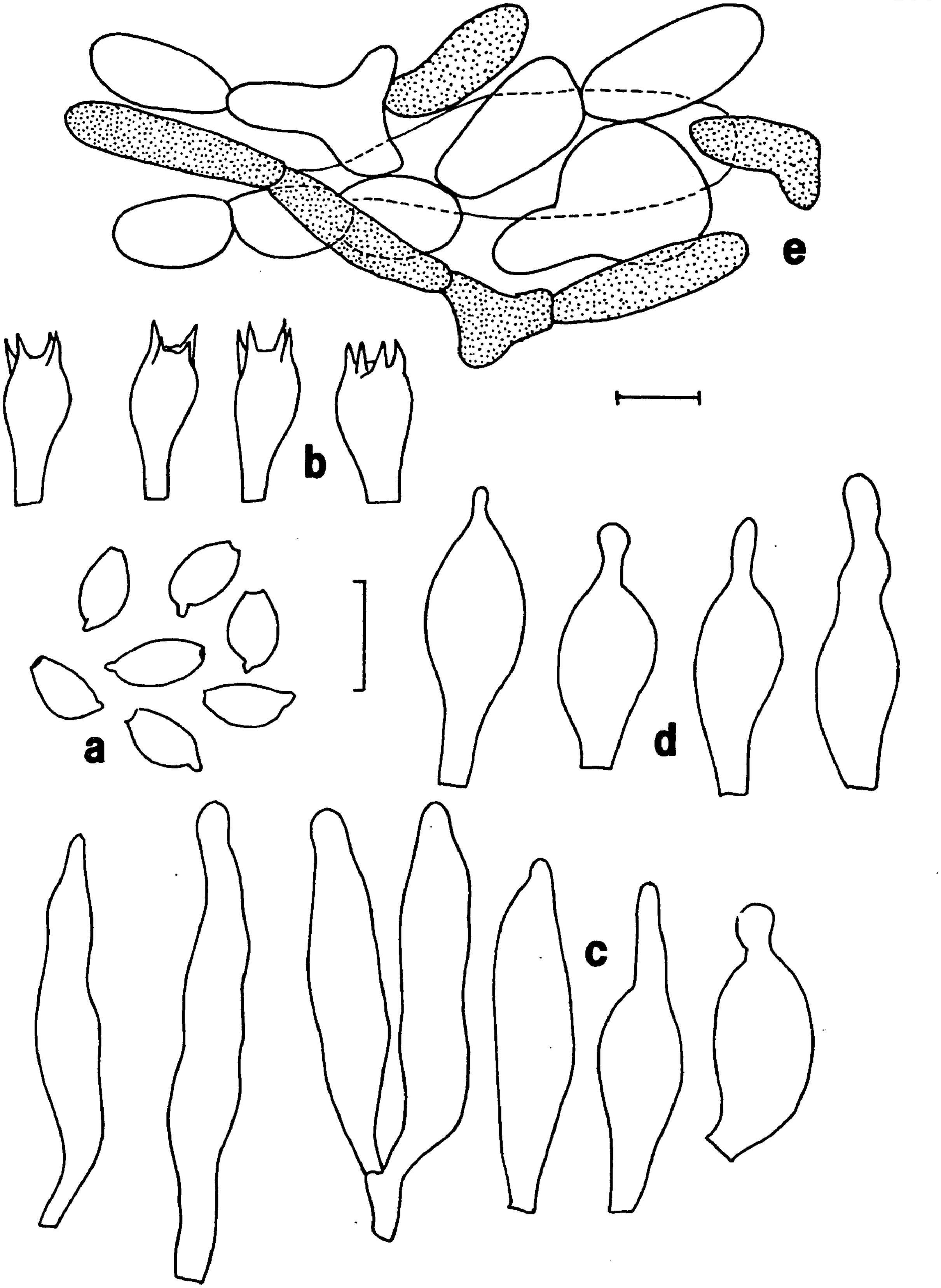
FIG. 20. _Leucocoprinus_ _sulphurellus_ (_Franco-M._ _583_). Habit (2X).

FIGS. 21a-e. Line drawings of the microscopic features of *Leucocoprinus sulphurellus* (*Franco-M. 583*). a. Basidiospores. b. Basidia. c. Cheilocystidia. d. Pleurocystidia. e. Pileipellis. Scale lines = 10 μm.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FIGS. 22a-c. Line drawings of the microscopic features of Leucocoprinus tenellus (Franco-M. 872). a. Pileipellis. b. Basidiospores. c. Basidia. Scale lines = 10 μm.

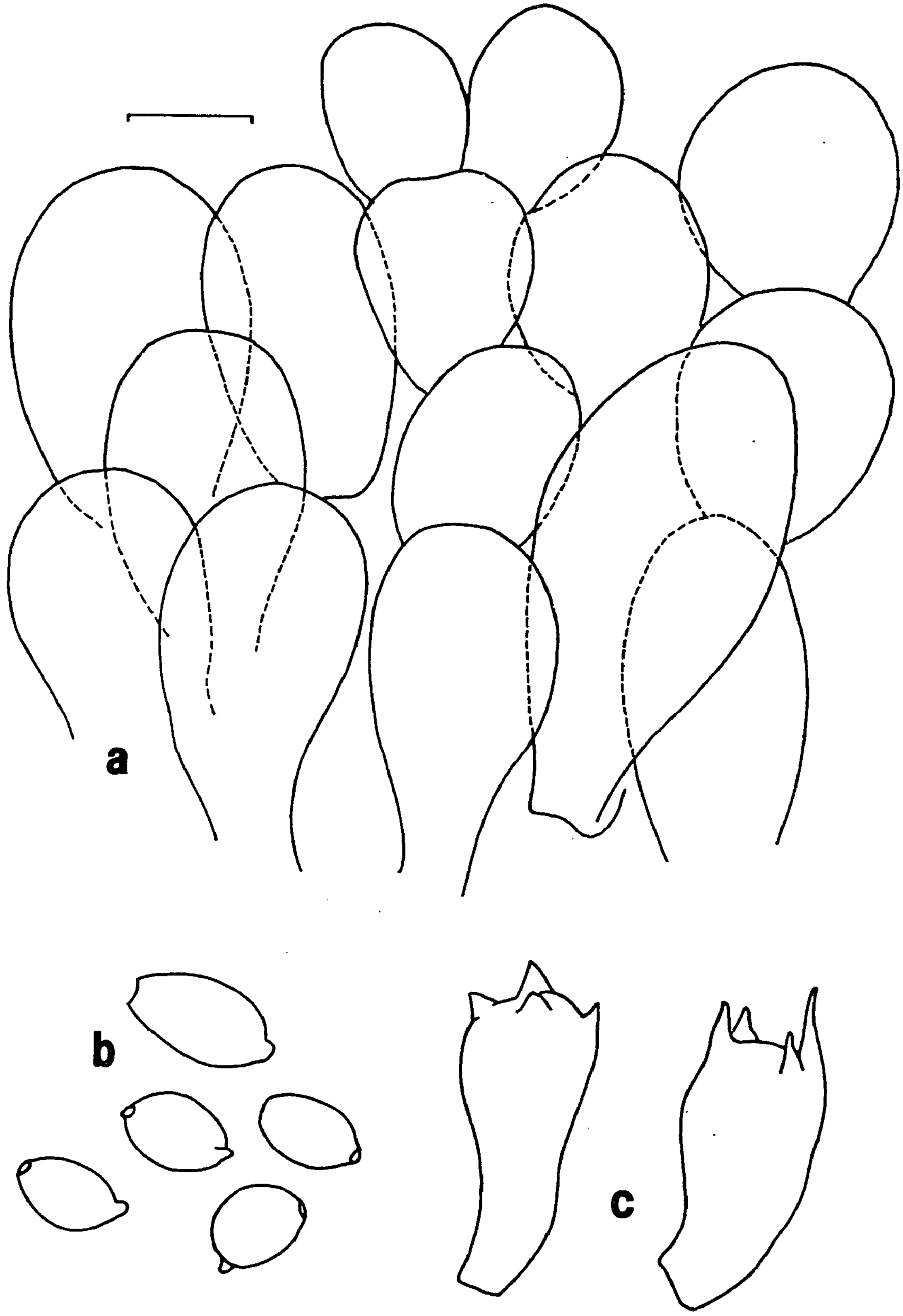
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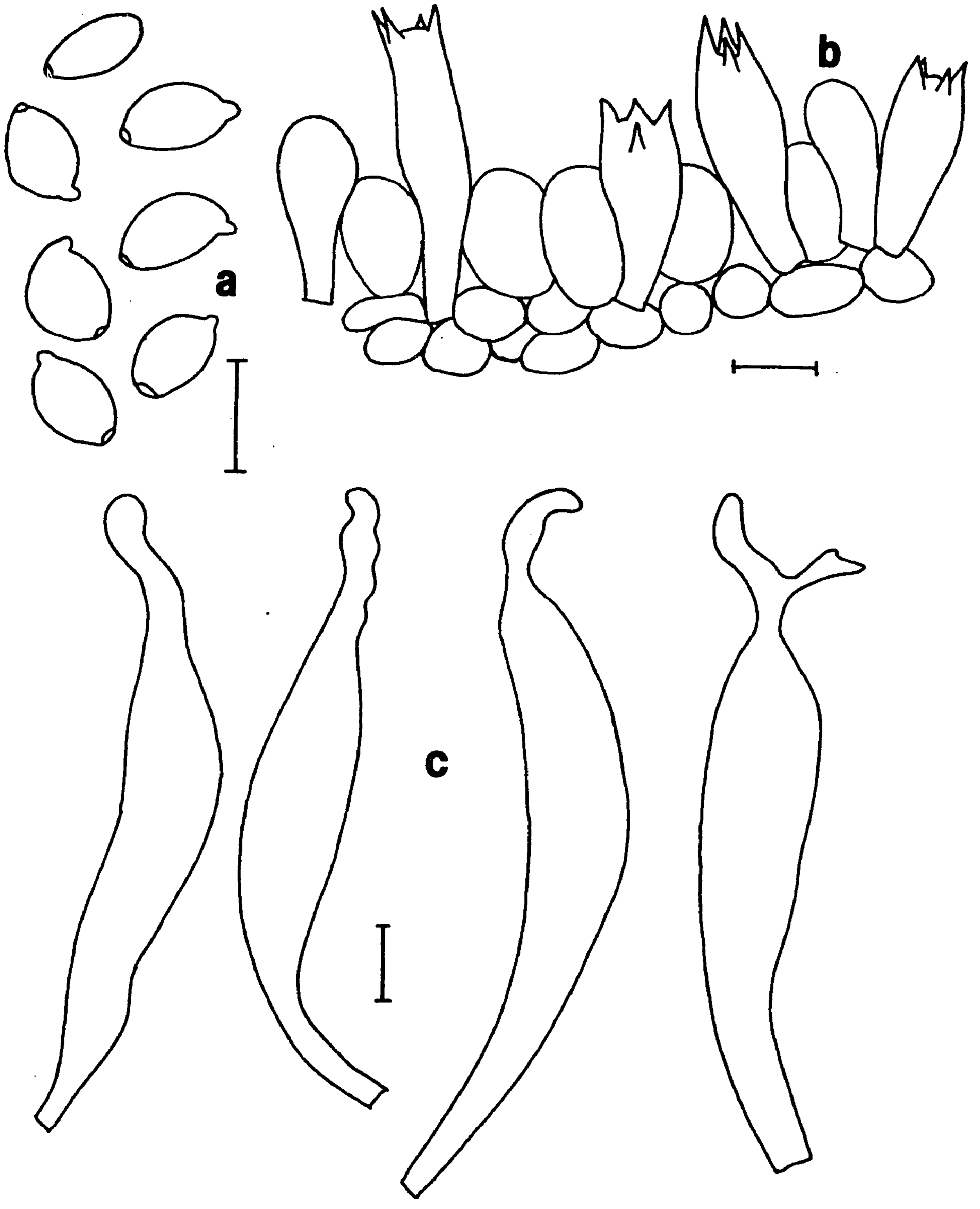
FIG. 23. *Leucocoprinus cepaestipes* (*Franco-M. 545*). Habit (1X).

FIGS. 24a-e. Line drawings of the microscopic features of *Leucocoprinus cepaestipes* (*Franco-M. 545*). a. Basidiospores. b. Basidia and paraphyses. c. Cheilocystidia. d. Pileipellis. e. Stipitipellis. Scale lines = 10 μm.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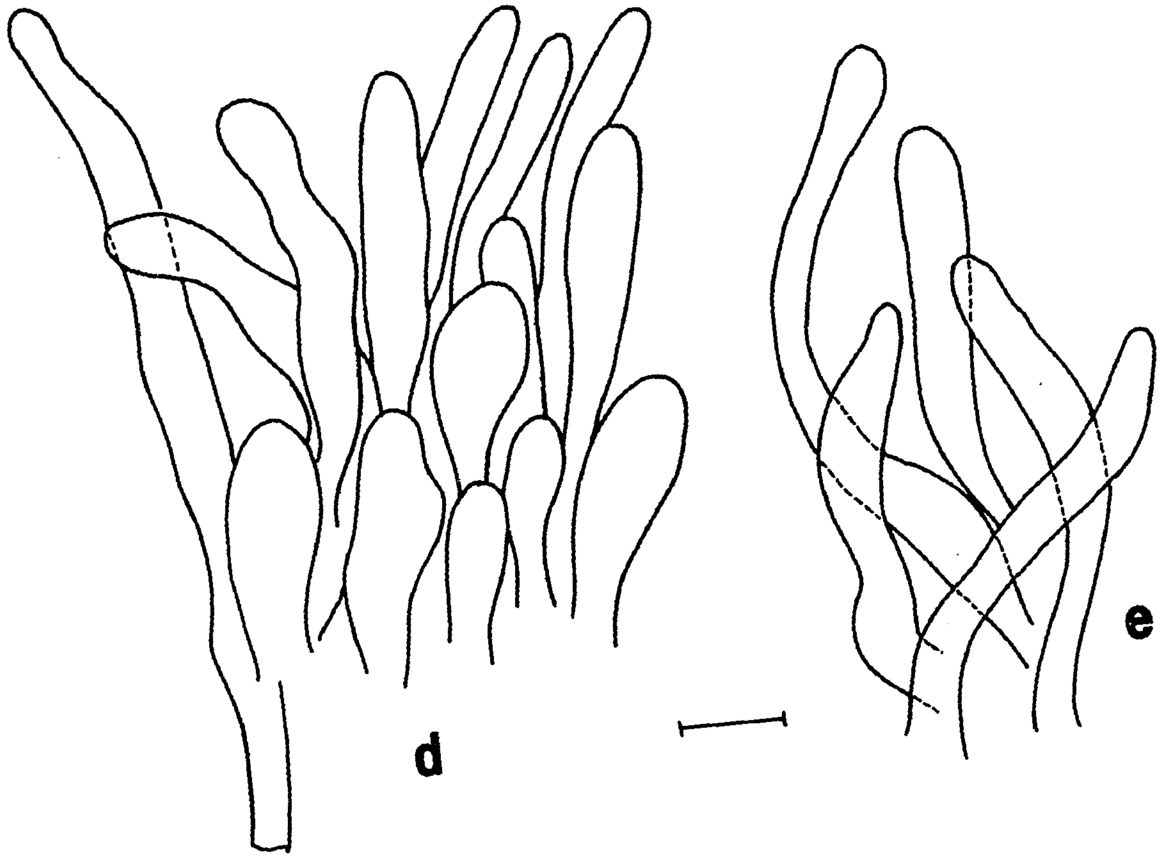
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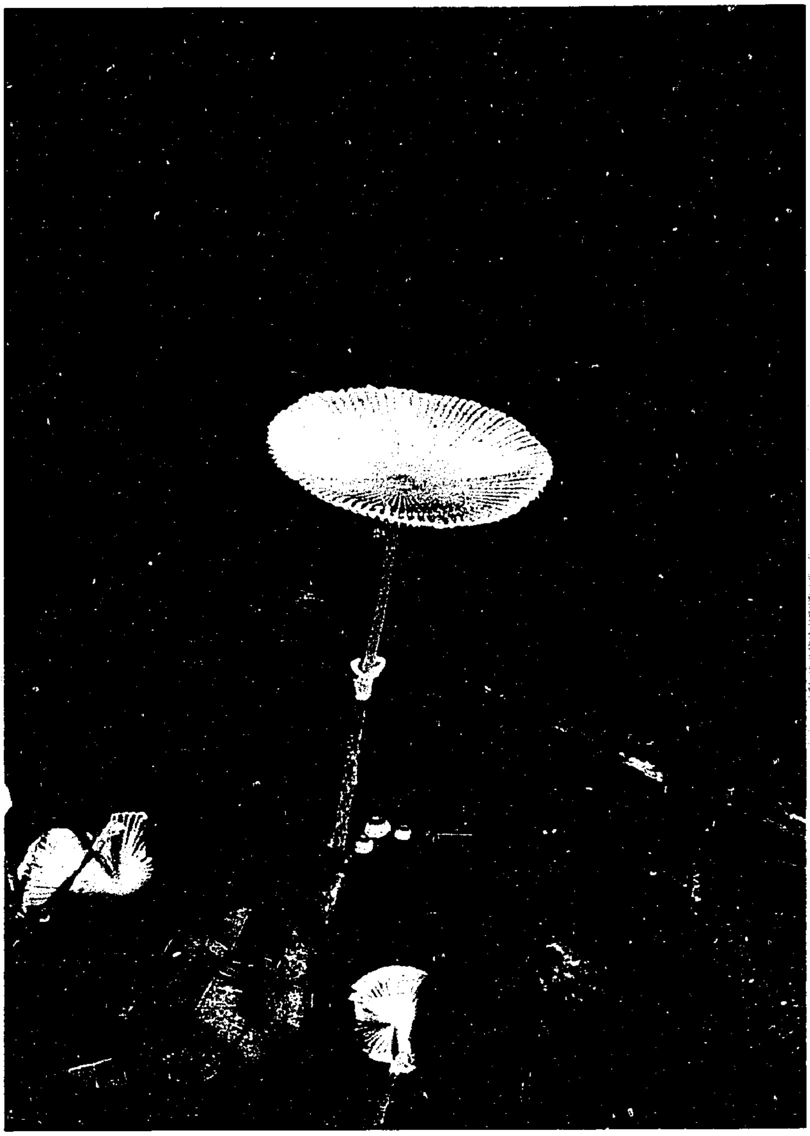
FIG. 25. *Leucocoprinus fragilissimus* (*Franco-M. 582*). Habit (±1/2X).



FIGS. 26a-f. Line drawings of the microscopic features of *Leucocoprinus fragilissimus* (*Franco-M. 582*). a. Cheilocystidia. b. Basidia and paraphyses. c. Suprapileipellis. d. Annulus. e. Subpileipellis. f. Basidiospores. Scale lines = 10 μm.

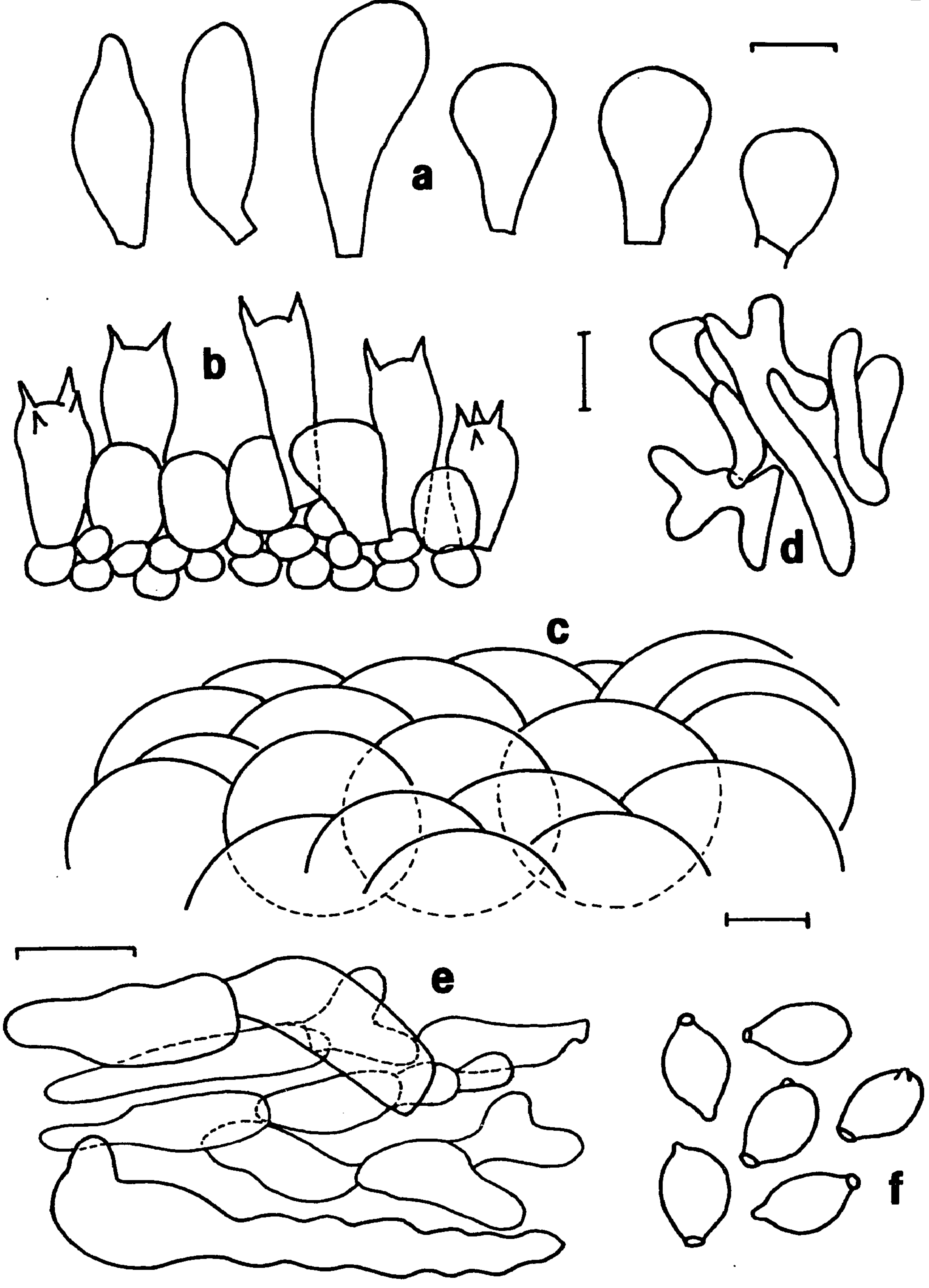

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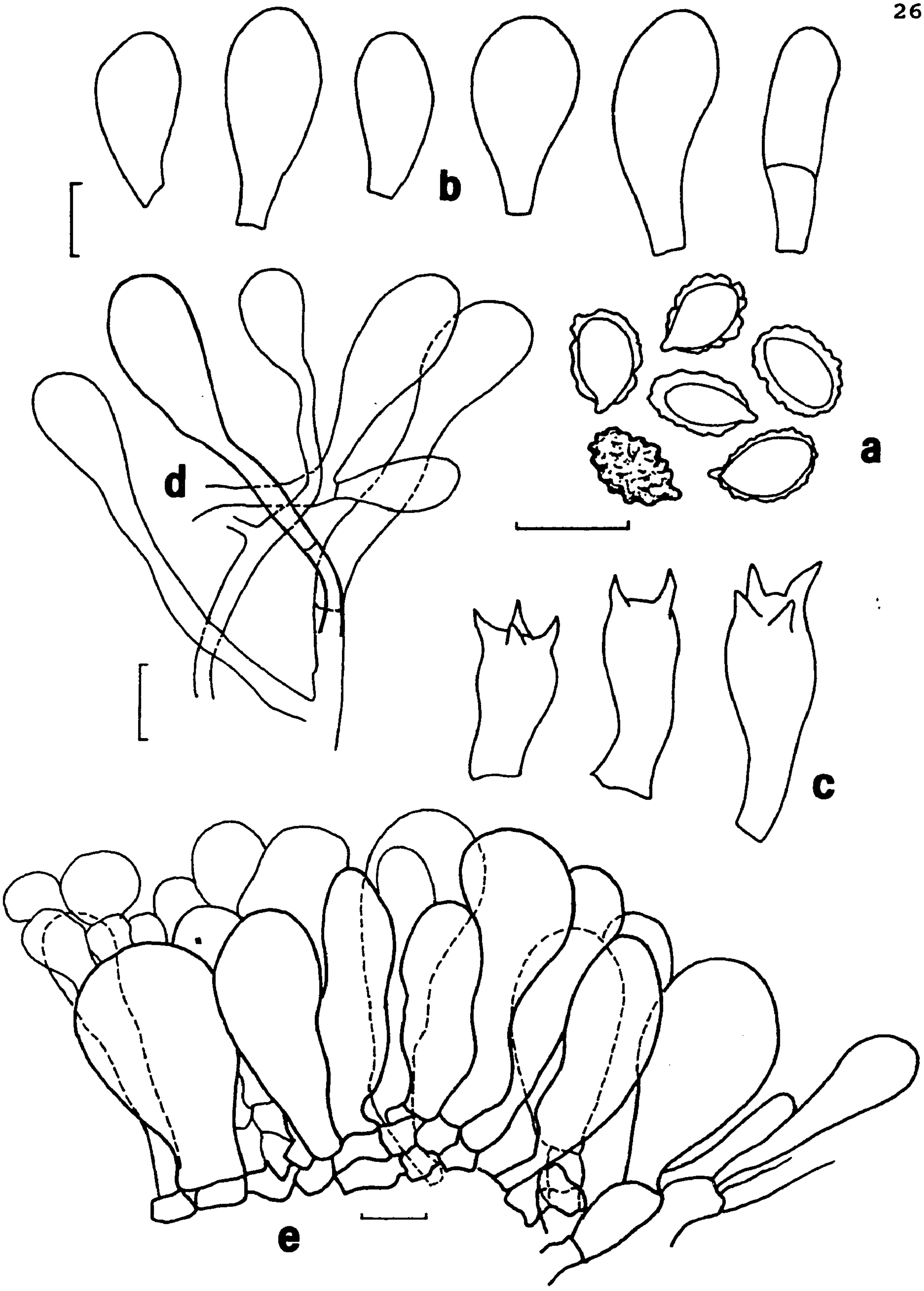
FIG. 27. *Rugosospora pseudorubiginosa* (*Franco-M. 383*). Habit (1X).

FIGS. 28a-e. Line drawings of the microscopic features of Rugosospora pseudorubiginosa (Franco-M. 383). a. Basidiospores. b. Cheilocystidia. c. Basidia. d. Annulus, outerside hyphae. e. Pileipellis. Scale lines = 10 μm.


b
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e

FIGS. 29a-c. SEM microphotographies of basidiospores. a-b. Rugosospora pseudorubiginosa (Franco-M. 383). c. R. ochraceobadia (Goossens-Fontana 665). Scale lines = 1 μm in a; 2 μm in b and c.

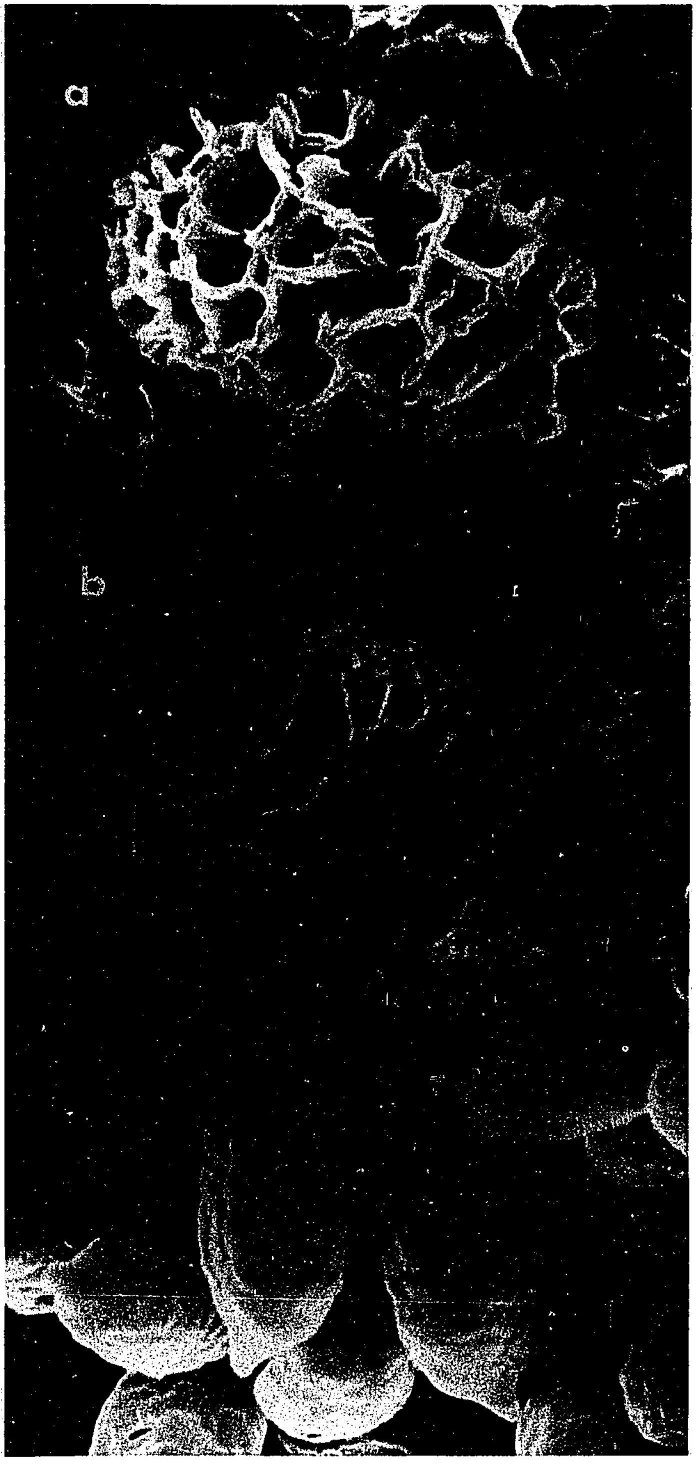
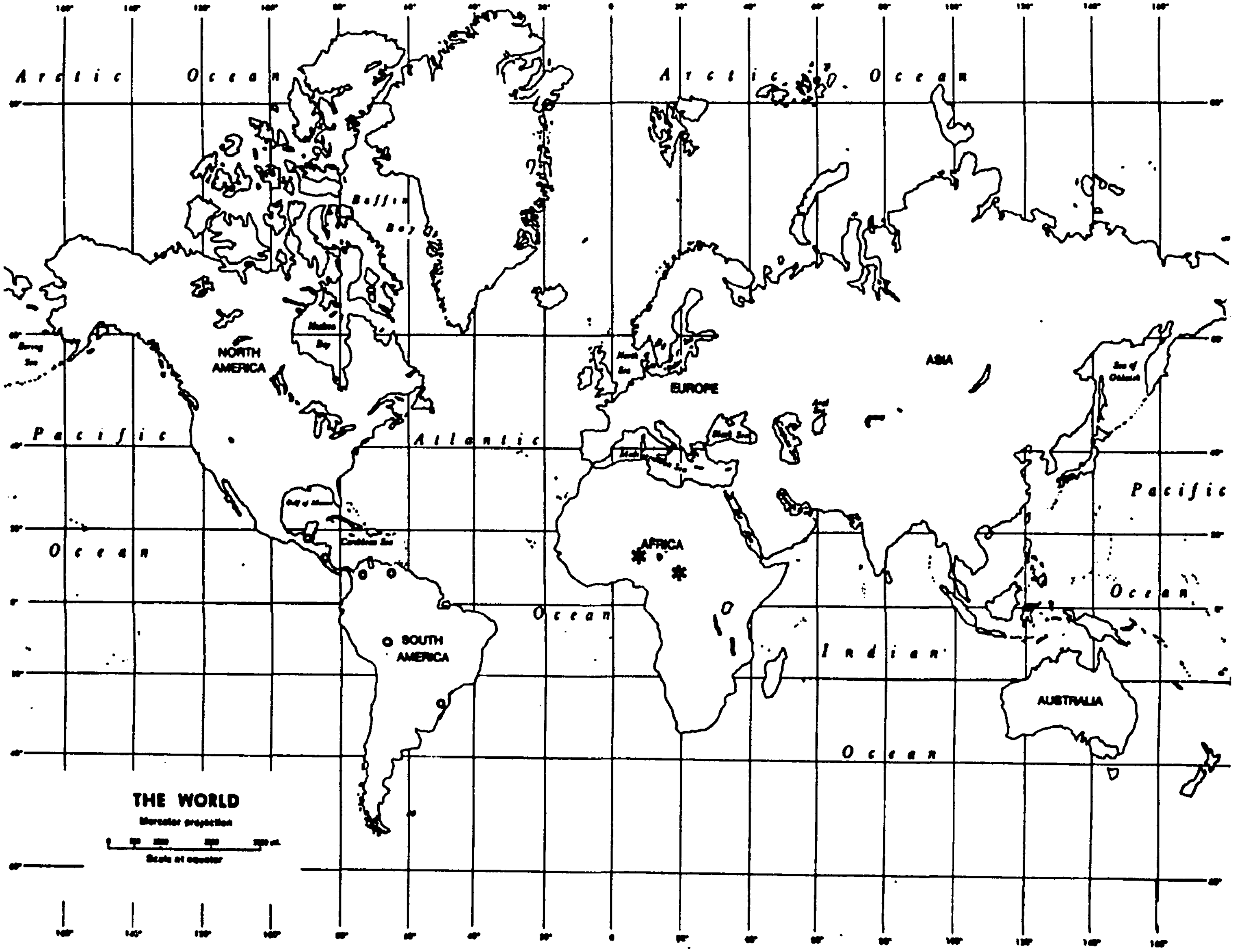

a
b

FIG. 30. Distribution of *Rugosospora*. Circles indicate *R. psudorubiginosa*, stars indicate *R. ochraceobadia*.

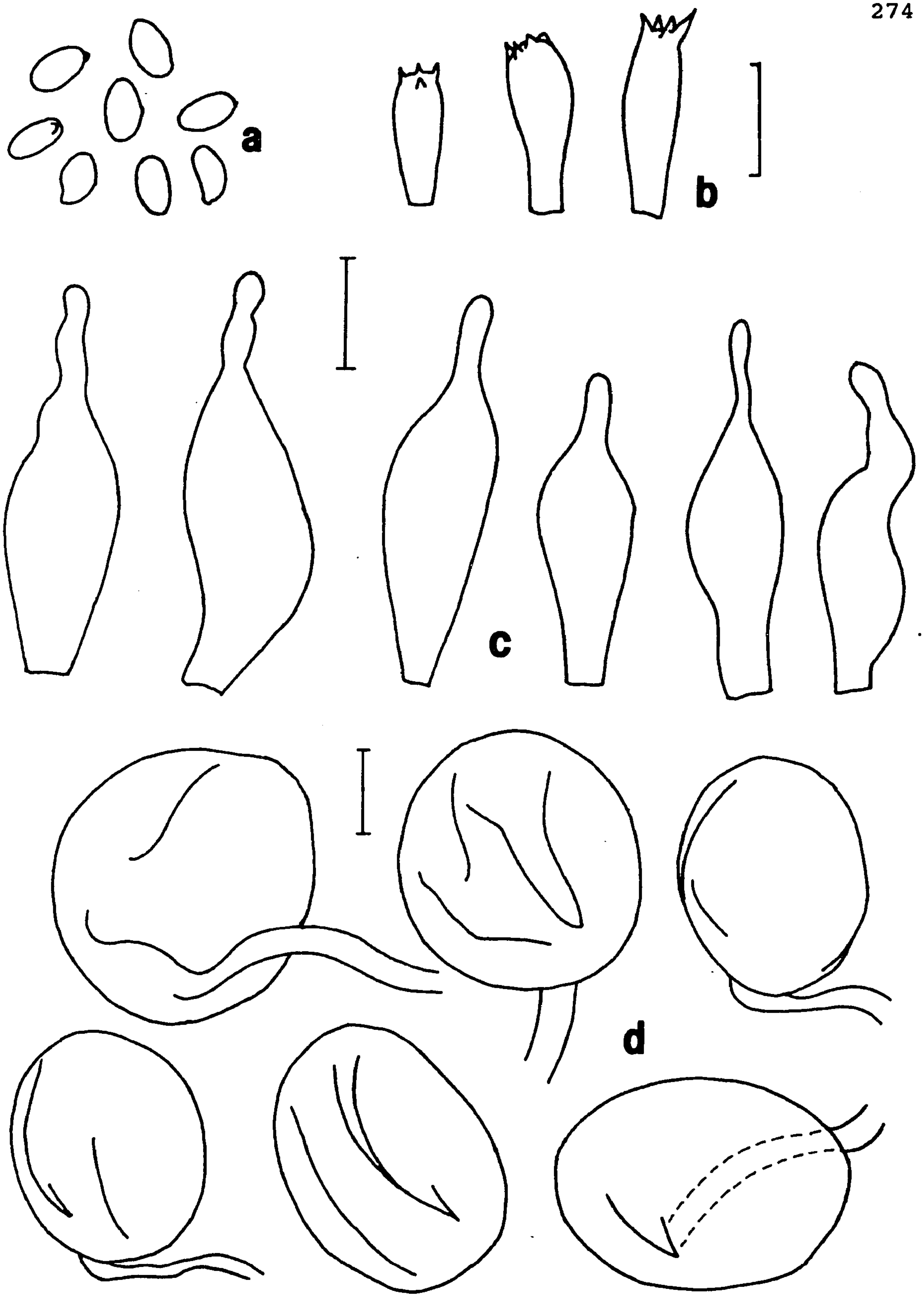


THE WORLD

Mercator projection

Scale at equator

FIGS. 31a-d. Line drawings of the microscopic features of Cystolepiota coquisorum (Franco-M. 987)a. Basidiospores. b. Basidia. c. Pleurocystidia and Cheilocystidia. d. Pileipellis elements. Scale lines = 10 µm.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FIGS. 32a-d. Line drawings of the microscopic features of *Lepiota bisporigera* (*Franco-M. 137*). a. Basidiospores. b. Basidia. c. Cheilocystidia. d. Pileipellis elements. Scale lines = 10 μm.

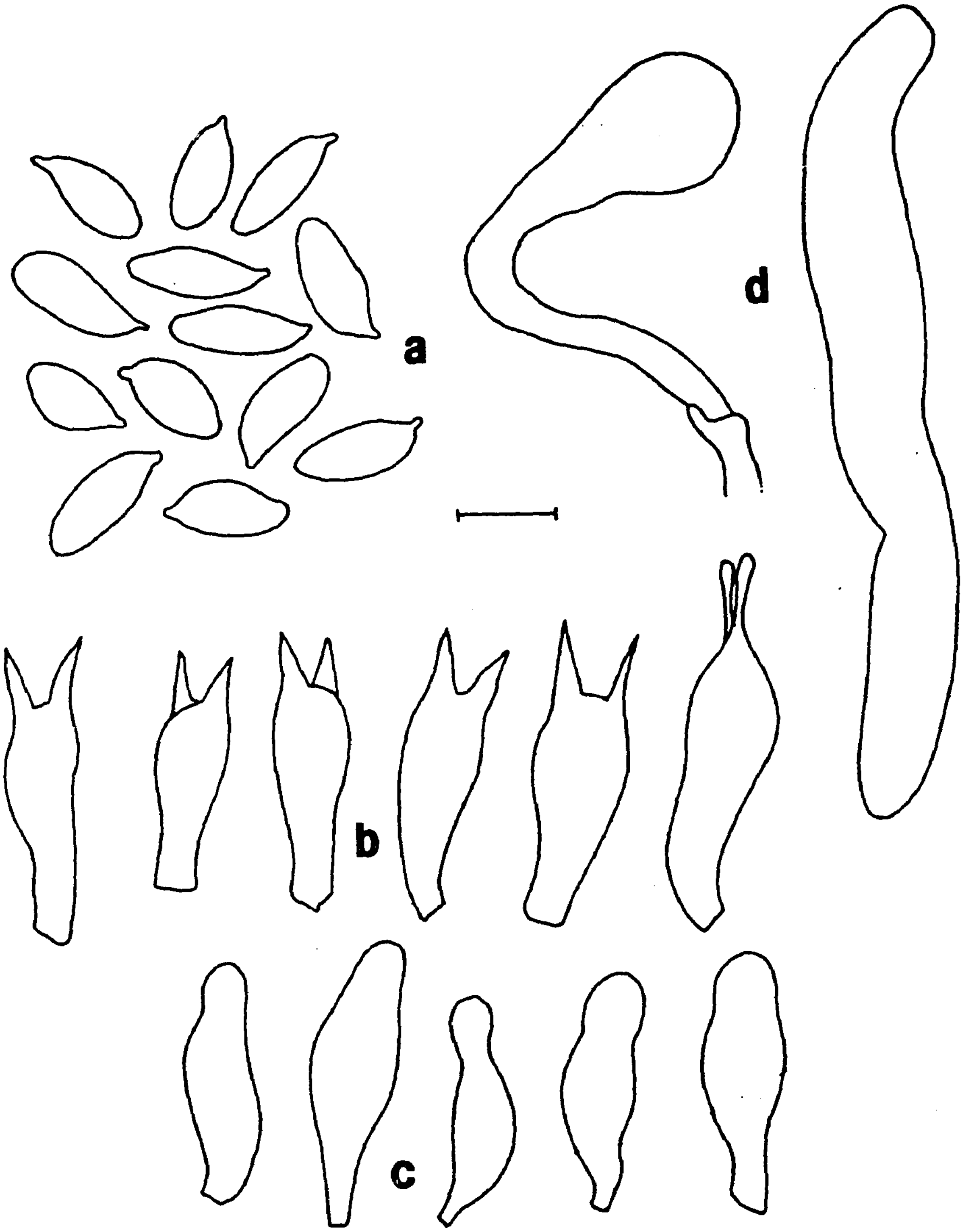
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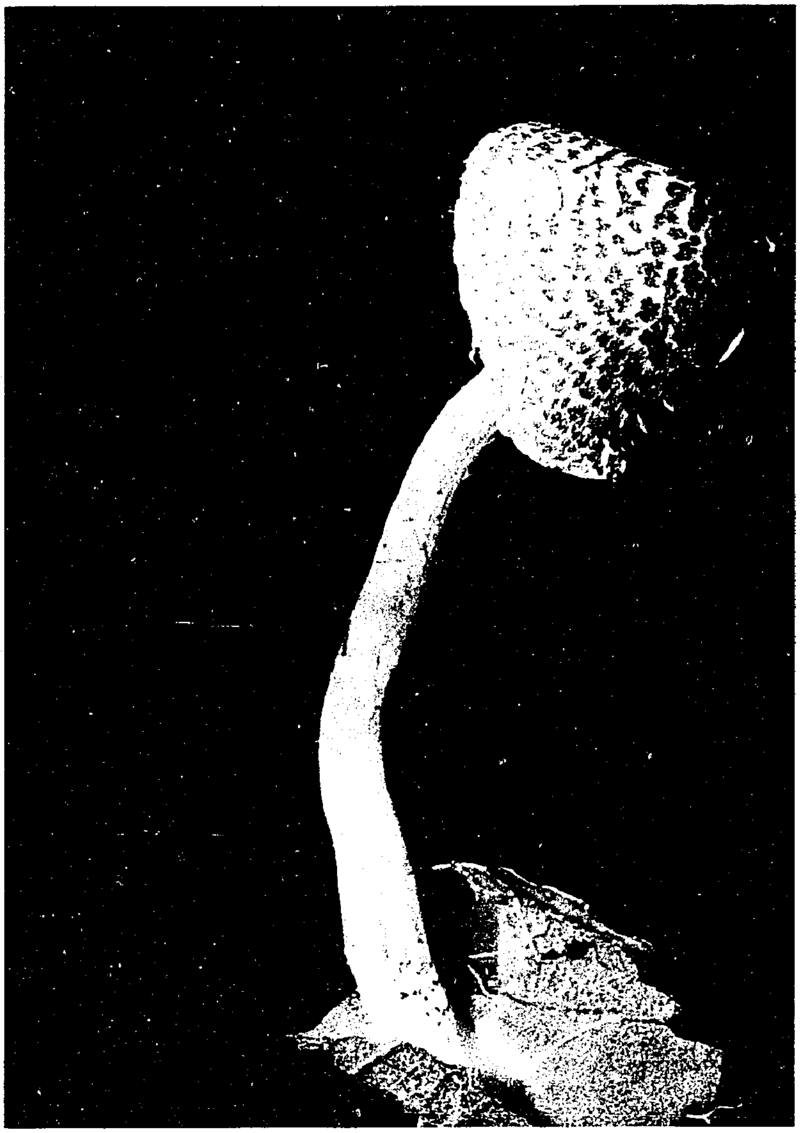
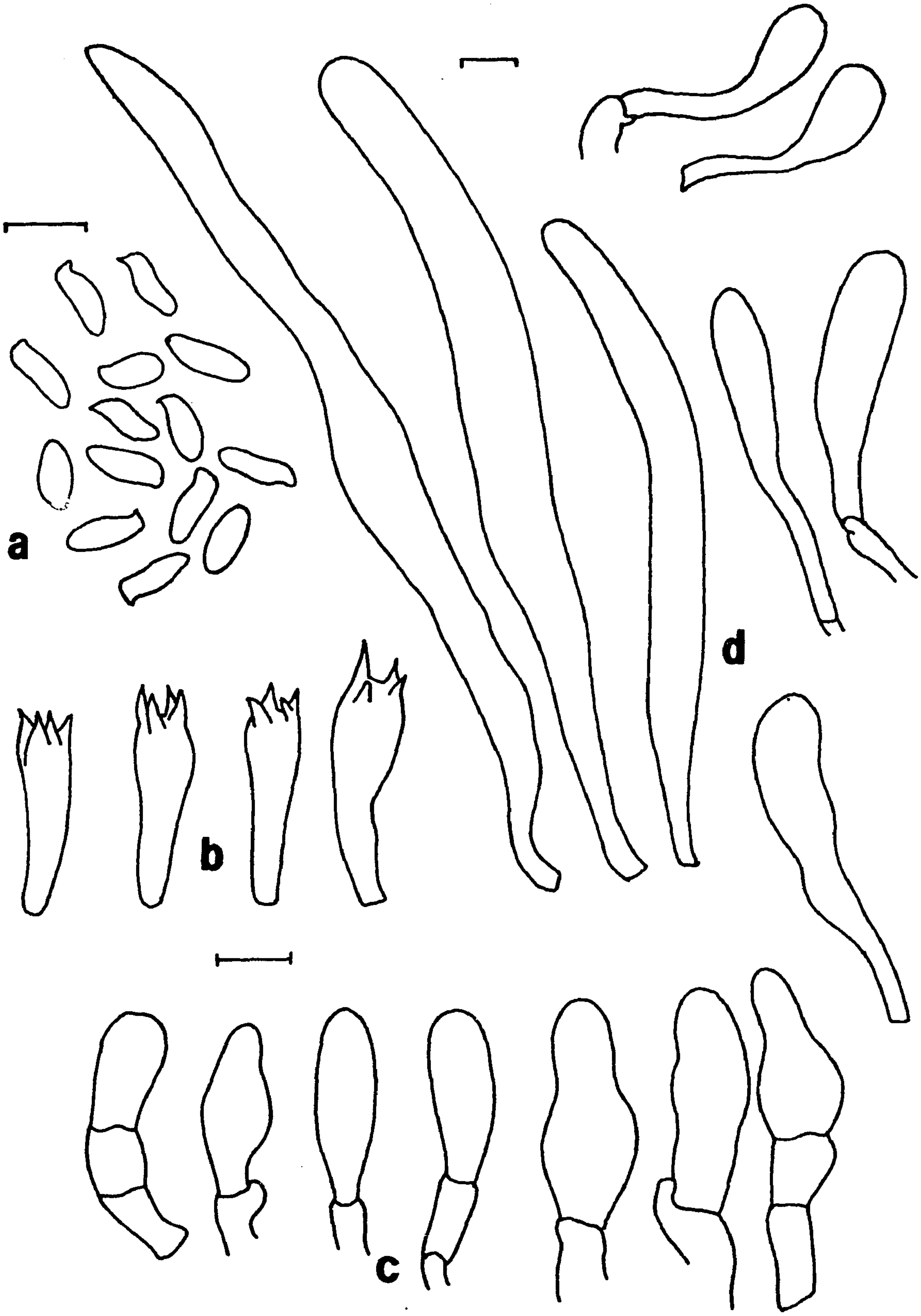
FIG. 33. *Lepiota theobromicola* (*Franco-M. 742*). Habit (±2X)



FIGS. 34a-d. Line drawings of the microscopic features of *Lepiota theobromicola* (Franco-M. 742). a. Basidiospores. b. Basidia. c. Cheilocystidia. d. Pileipellis elements. Scale lines = 10 μm.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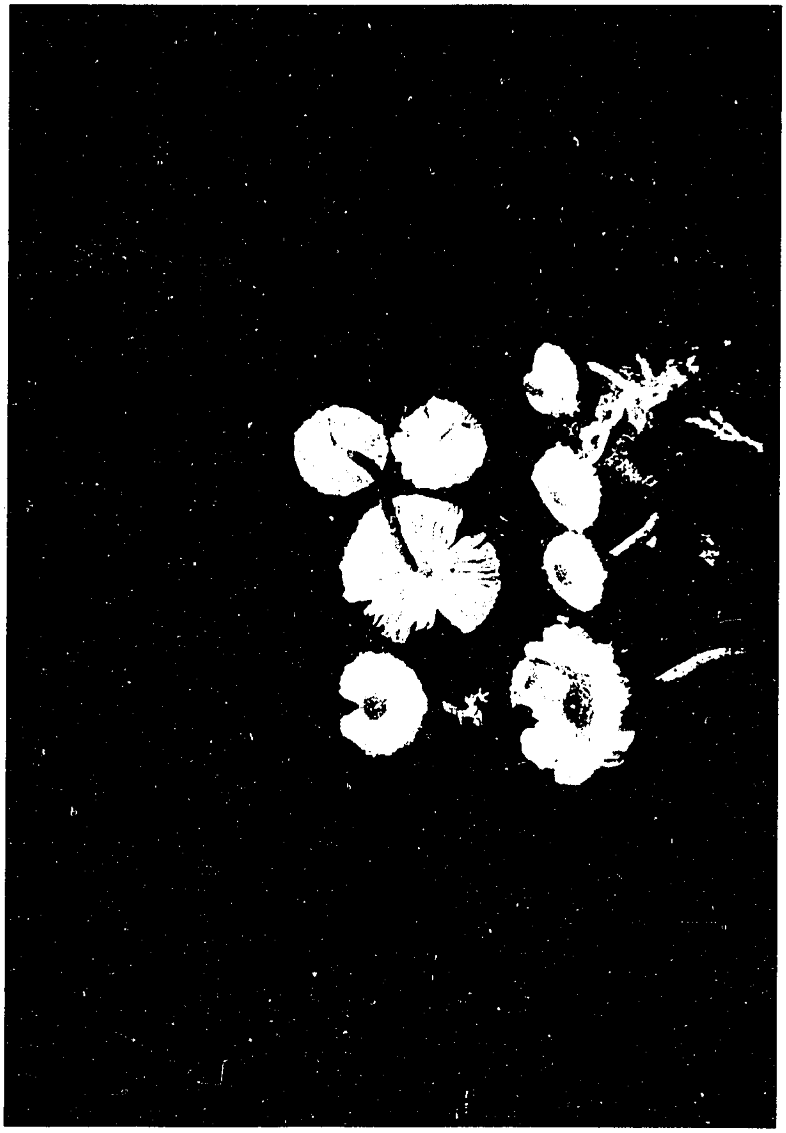
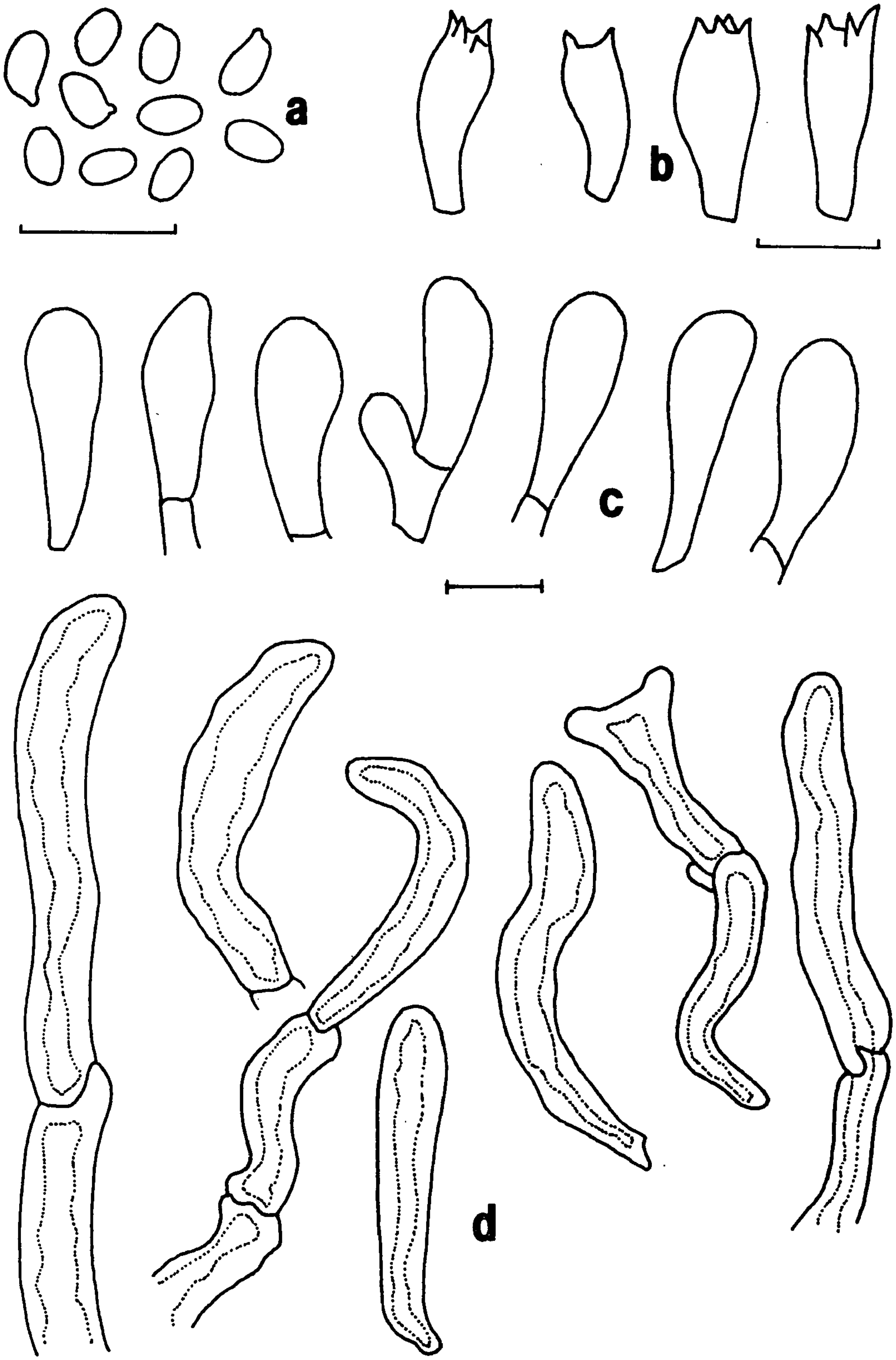
FIGS. 35. *Lepiota bettinae* (*Franco-M. 978*). Habit (±1X).



FIGS. 36a-d. Line drawings of the microscopic features of *Lepiota bettinae* (*Franco-M. 978*). a. Basidiospores. b. Basidia. c. Cheilocystidia. d. Pileipellis elements. Scale lines = 10 μm.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FIGS. 37a-d. Line drawings of the microscopic features of *Lepiota narinyensis* (*Franco-M. 179*). a. Cheilocystidia. b. Basidiospores. c. Basidia. d. Pileipellis. Scale lines = 10 μm.

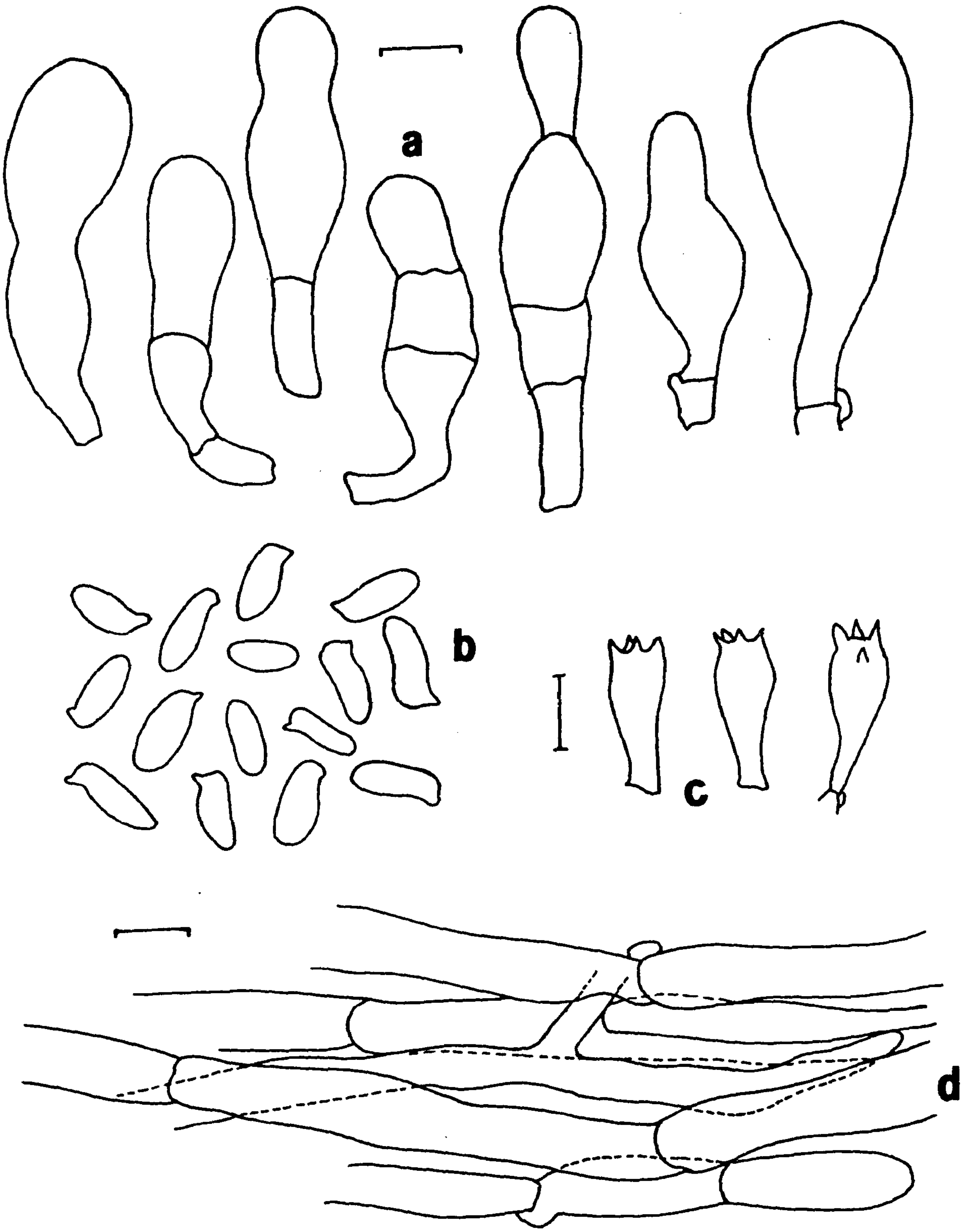
a
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FIG. 38. *Lepiota azalearum* (*Franco-M. 717*). Habit (±2X).

FIGS. 39a-e. Line drawings of the microscopic features of _Lepiota_ _azalearum_ (_Franco-M._ _717_). a. Basidiospores. b. Basidia. c. Cheilocystidia. d. Pileipellis elements. e. Annulus elements. Scale lines = 10 μm in a,b, and c; = 20 μm in d and e.

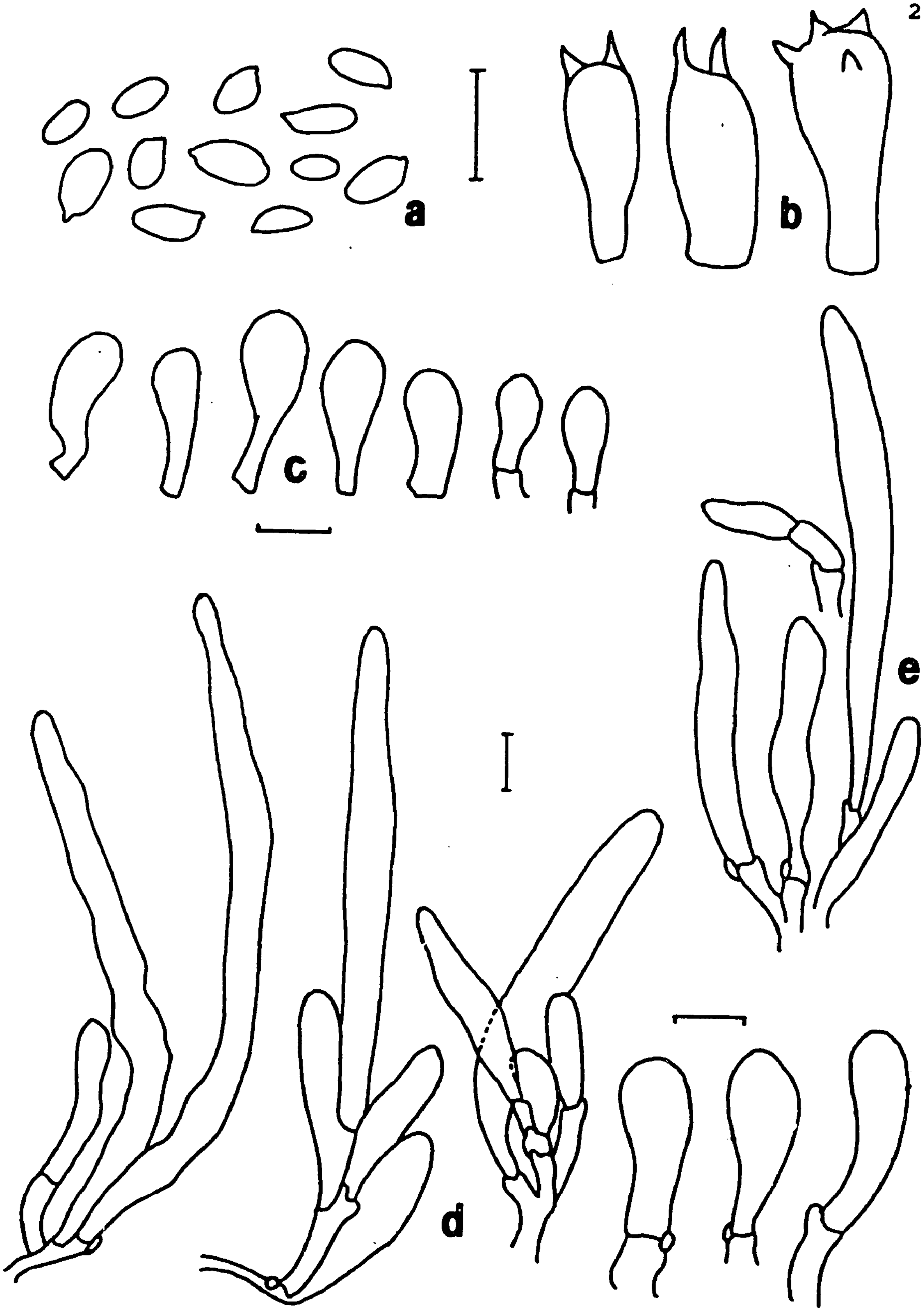
a
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FIG. 40. _Lepiota erythrosticta_ (_Franco-M. 385_). Habit (±2X).

FIGS. 41a-d. Line drawings of the microscopic features of Lepiota erythrosticta (Franco-M. 385). a. Basidiospores. b. Basidia. c. Cheilocystidia. d. Pileipellis elements. Scale lines = 10 μm.

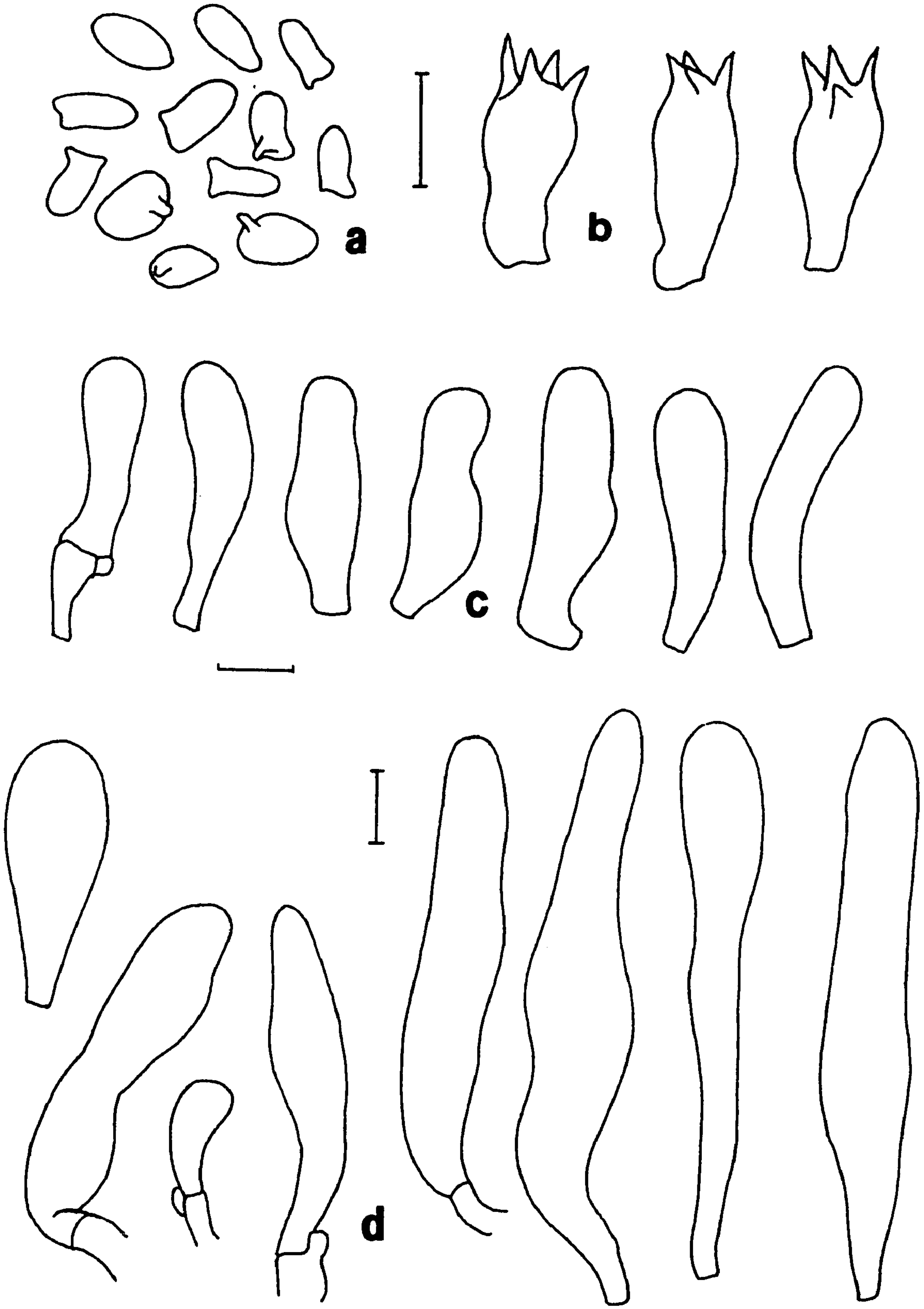
a
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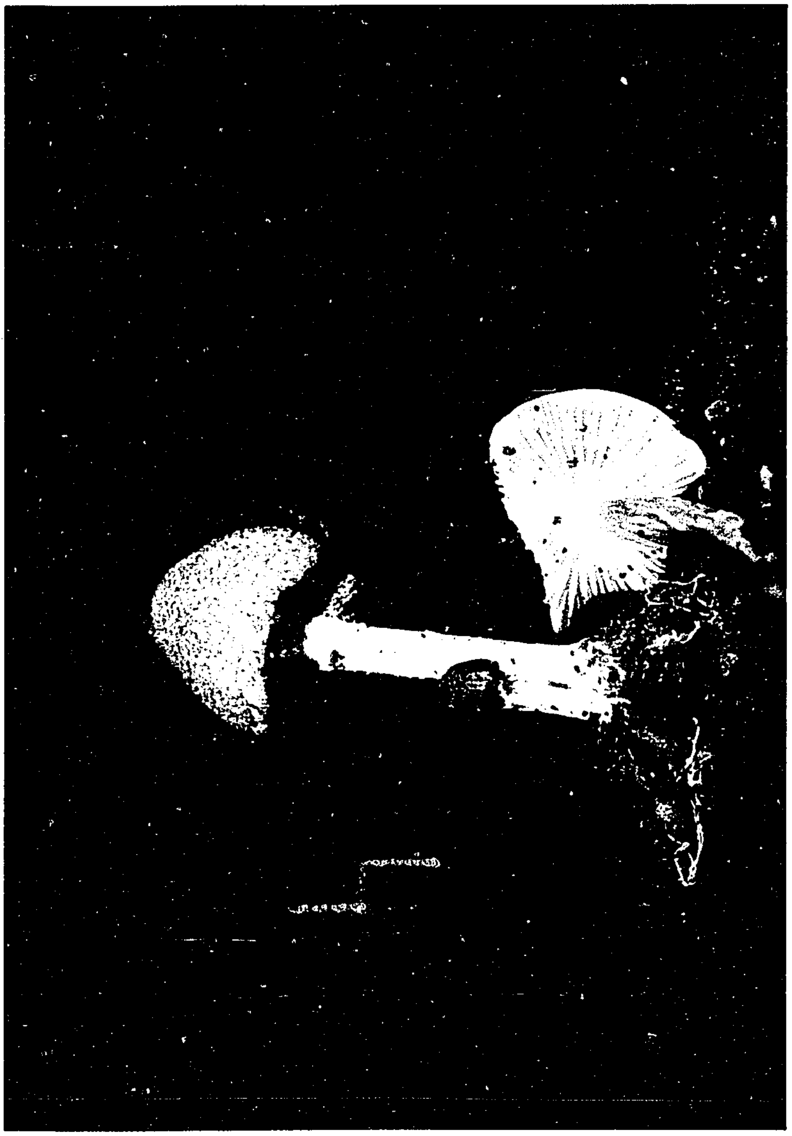
FIG. 42. _Lepiota_ _papillata_ (_Franco-M._ _798_). Habit (±3X).



FIGS. 43a-e. Line drawings of the microscopic features of *Lepiota papillata* (*Franco-M. 798*). a. Cheilocystidia. b. Basidiospores. c. Stipitipellis elements. d. Basidia. e. Pileipellis elements. Scale lines = 10 μm.

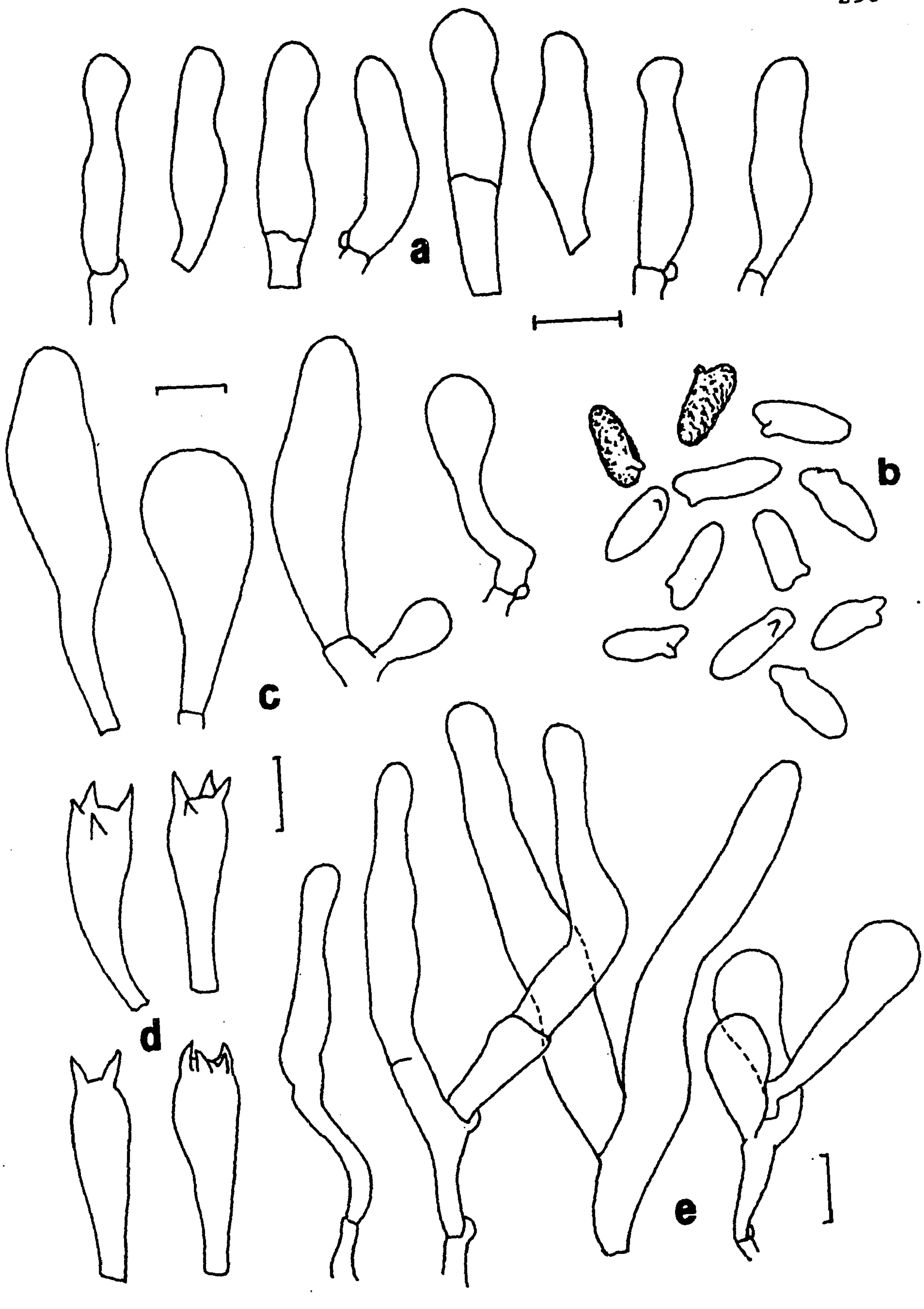

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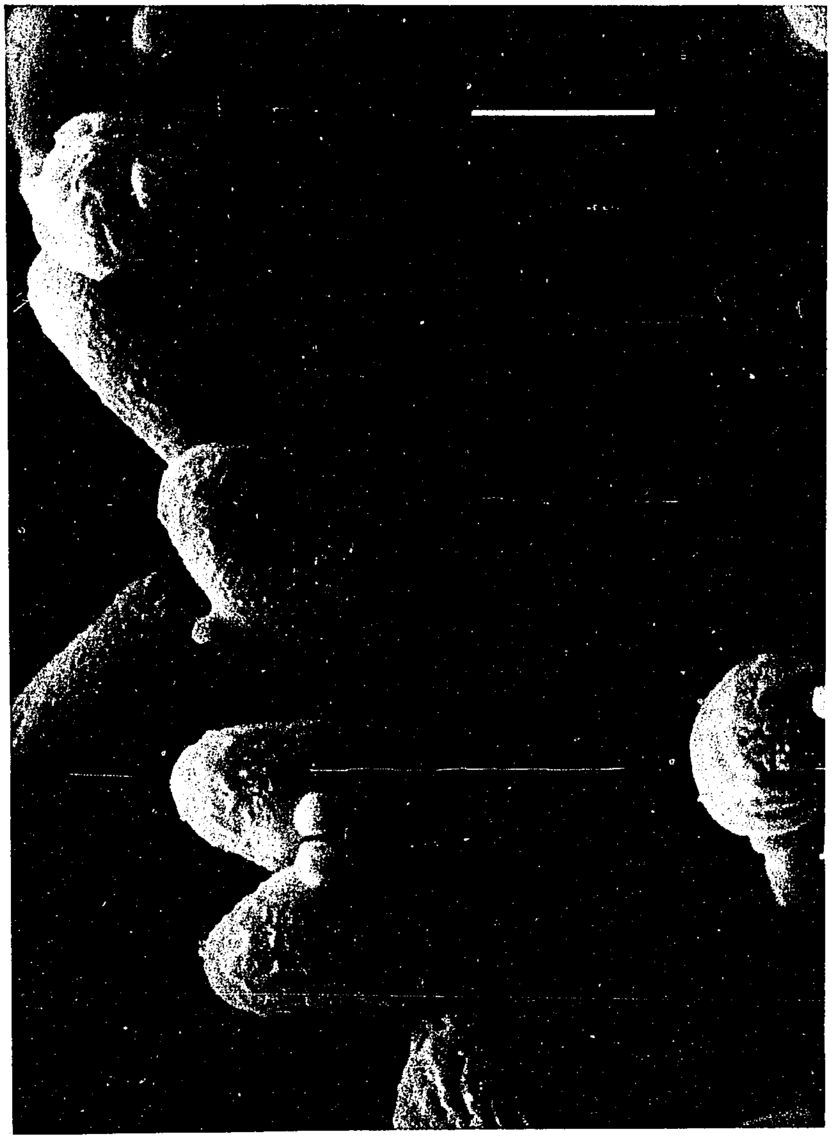
FIG. 44. Lepiota papillata (Franco-M. 798). SEM microphotography of basidiospores.



FIGS. 45a-e. Line drawings of the microscopic features of Lepiota sulphurocyanescens (Peñuela and Henao 742). a. Cheilocystidia. b. Basidia. c. Basidiospores. d. Pileipellis elements. e. Elements of annulus. Scale lines = 10 μm.

302

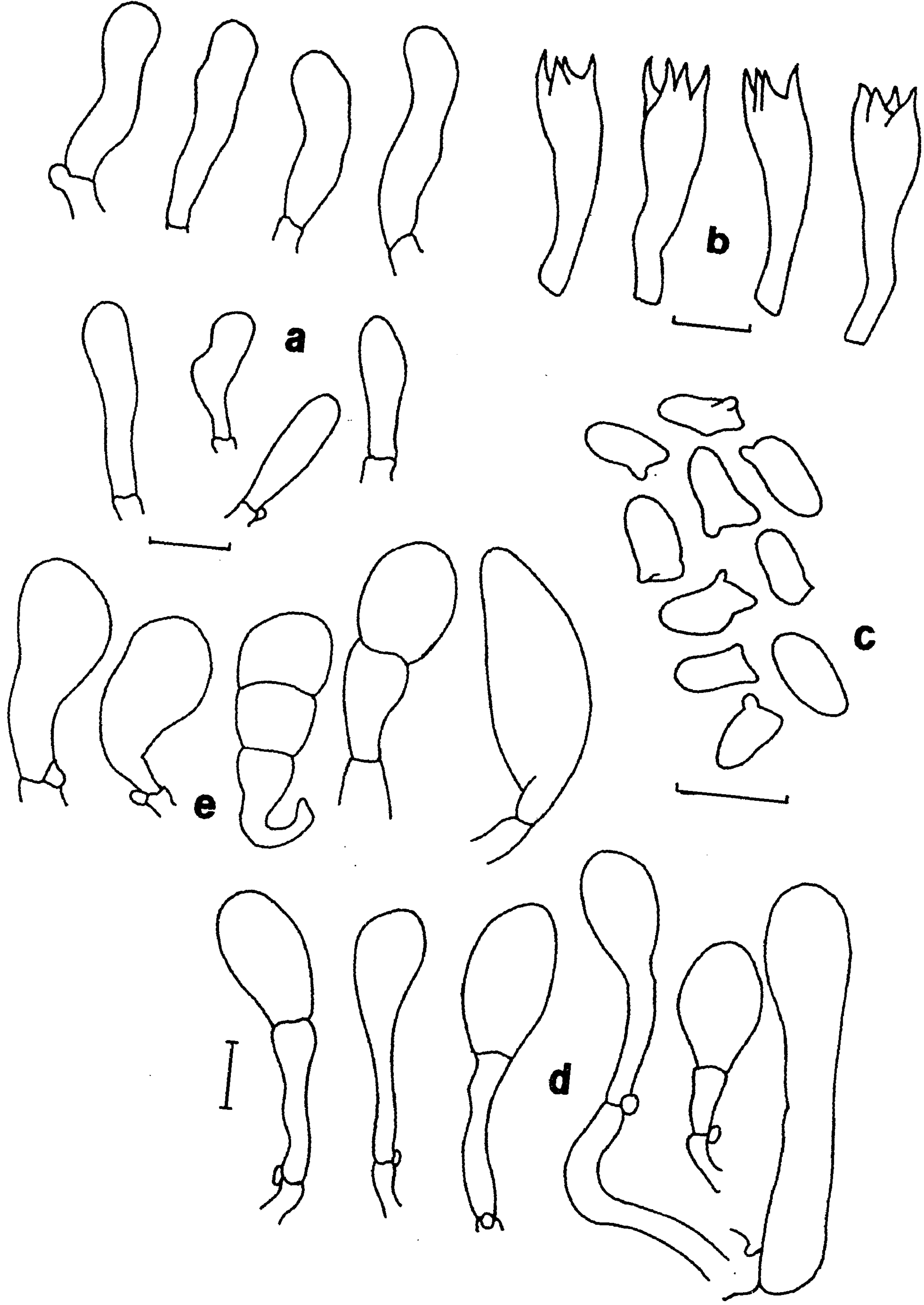
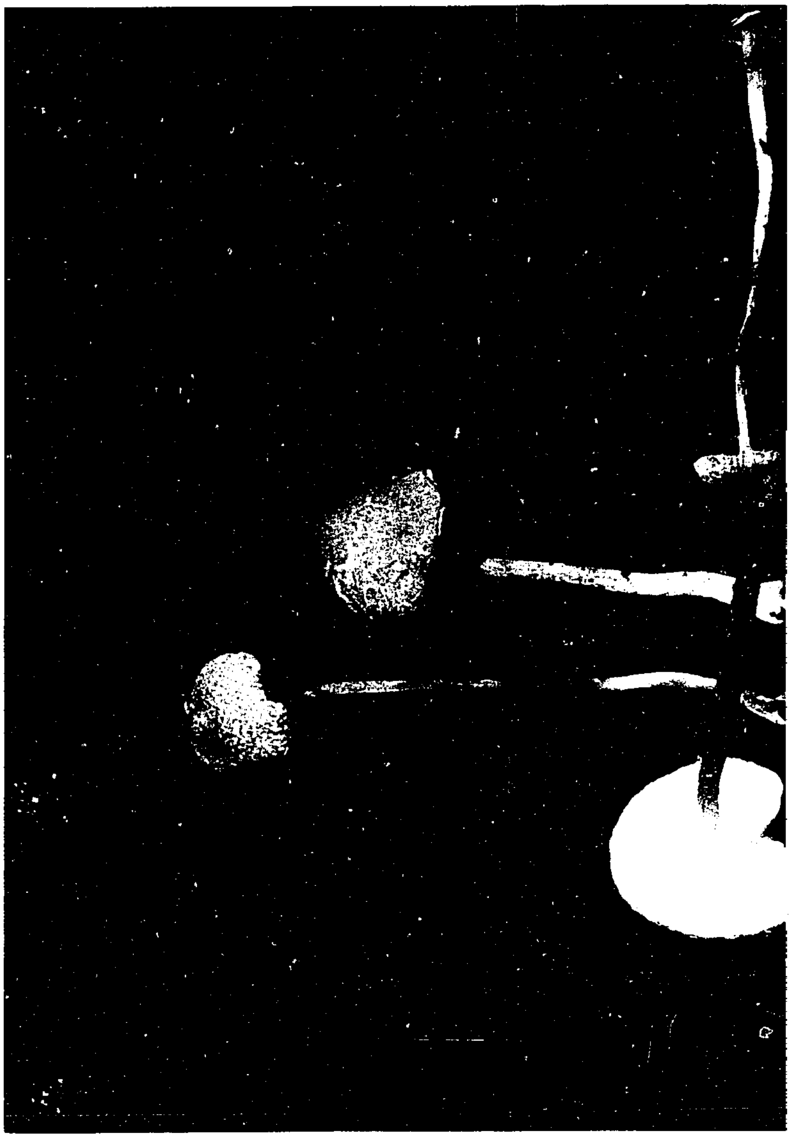


FIG. 46. *Lepiota pseudoignicolor* (*Franco-M. 727*). Habit (2X).



FIGS. 47a-d. Line drawings of the microscopic features of *Lepiota pseudoignicolor* (*Franco-M. 727*). a. Basidiospores. b. Basidia. c. Cheilocystidia. d. Pileipellis elements. Scale lines = 10 μm.

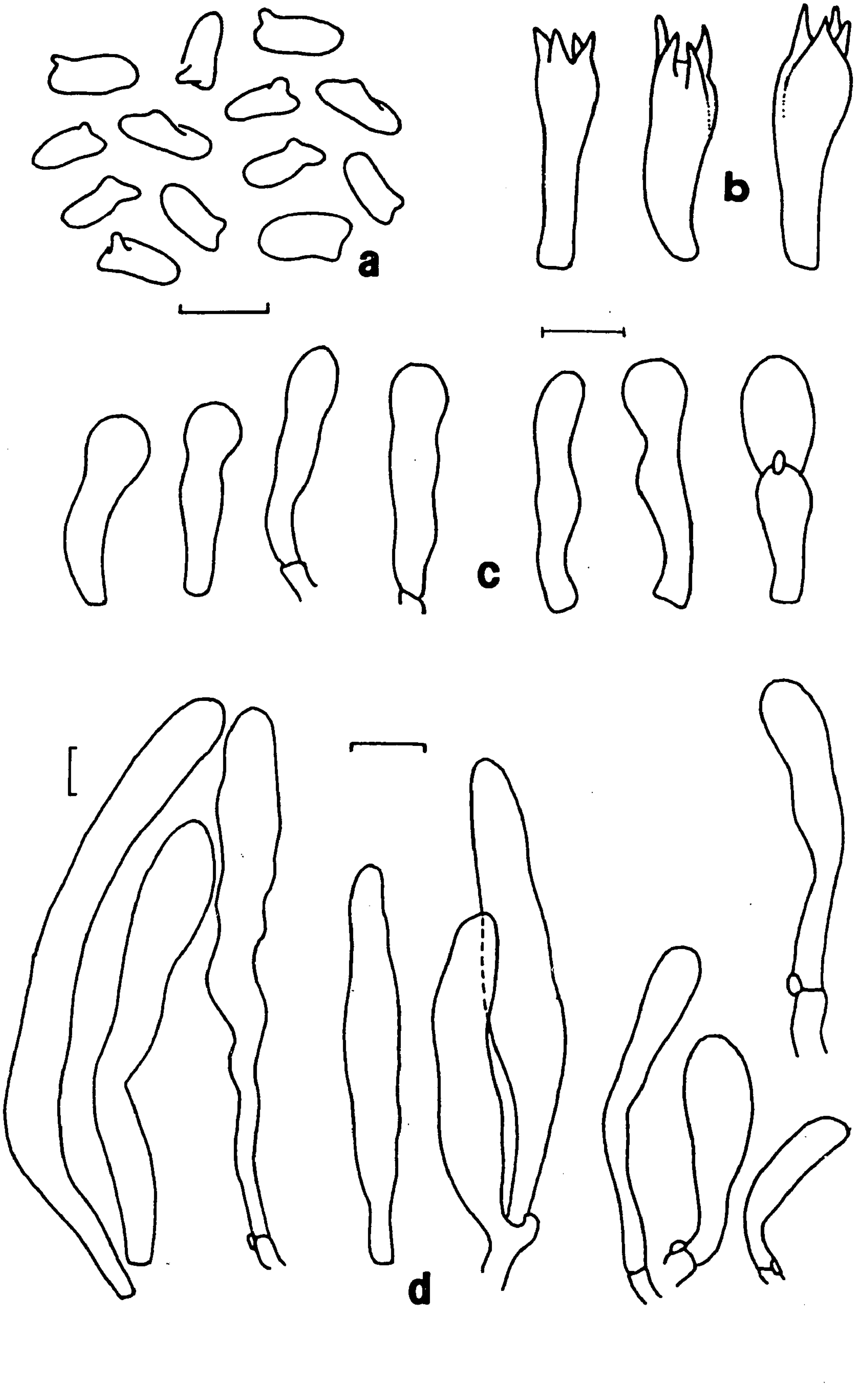

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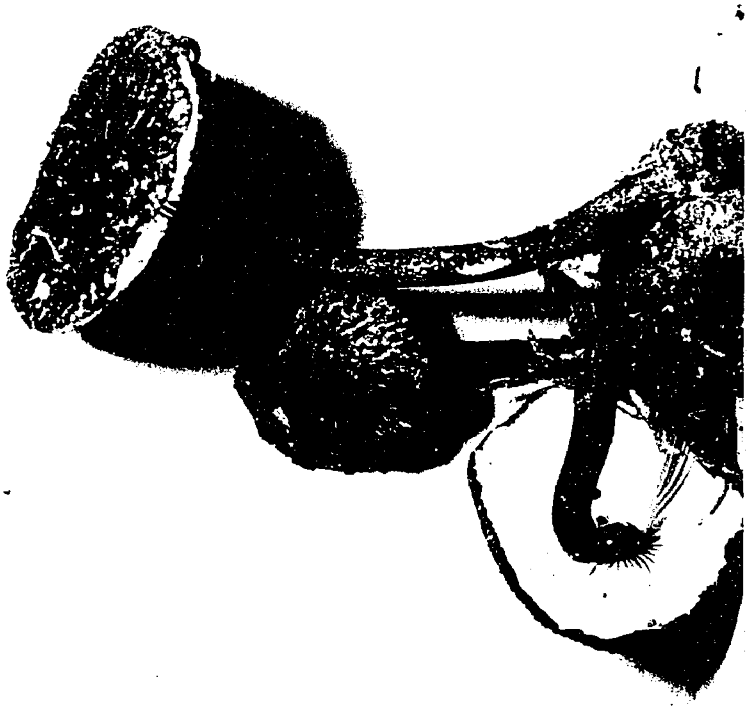
FIG. 48. *Lepiota belmirensis* (*Franco-M. 918*). Habit (±1X).



FIGS. 49a-e. Line drawings of the microscopic features of _Lepiota belmirensis_ (_Franco-M. 918_). a. Cheilocystidia. b. Basidiospores. c. Basidia. d. Pileipellis. e. Stipitipellis elements. Scale lines = 10 μm.

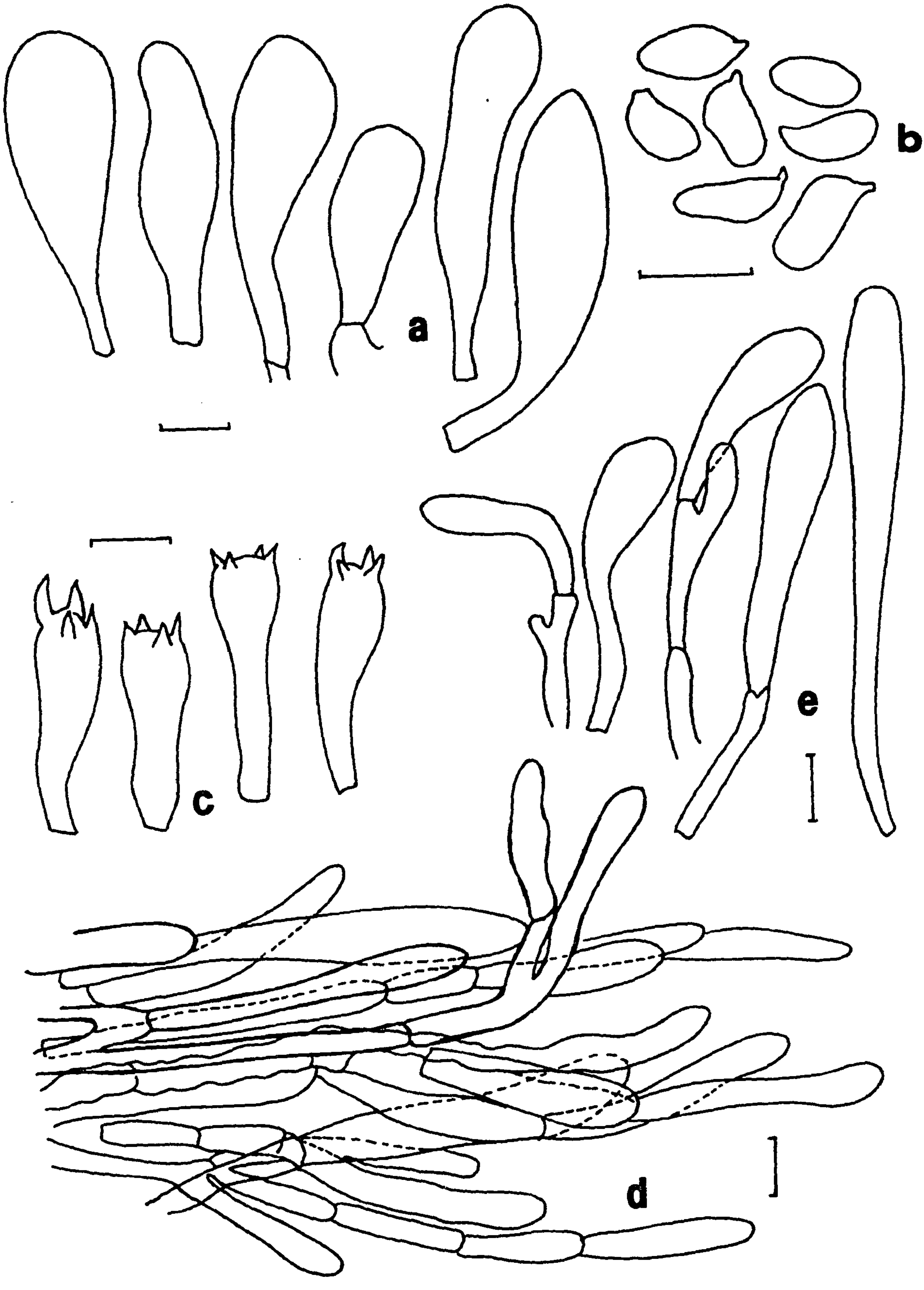

a
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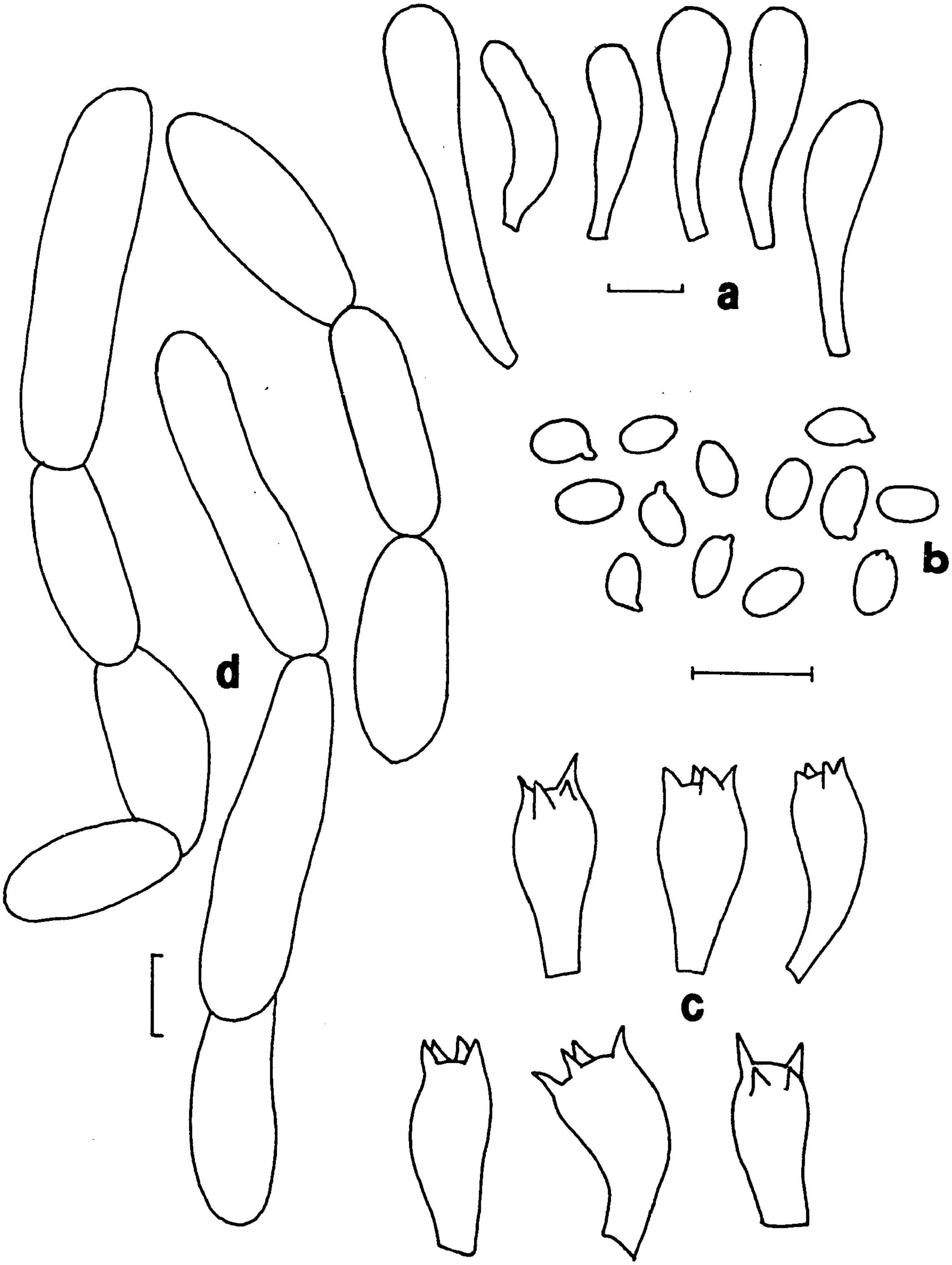
FIG. 50. Lepiota guatopoensis (Franco-M. 372). Habit (2X).

FIGS. 51a-d. Line drawings of the microscopic features of Lepiota guatopoensis (Franco-M. 372). a. Cheilocystidia. b. Basidiospores. c. Basidia. d. Pileipellis elements. Scale lines = 10 μm.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FIGS. 52a-d. Line drawings of the microscopic features of *Lepiota microcystidiata* (*Peñuela and Henao 674*). a. Basidiospores. b. Basidia. c. Pileipellis. Scale line = 10 μm.

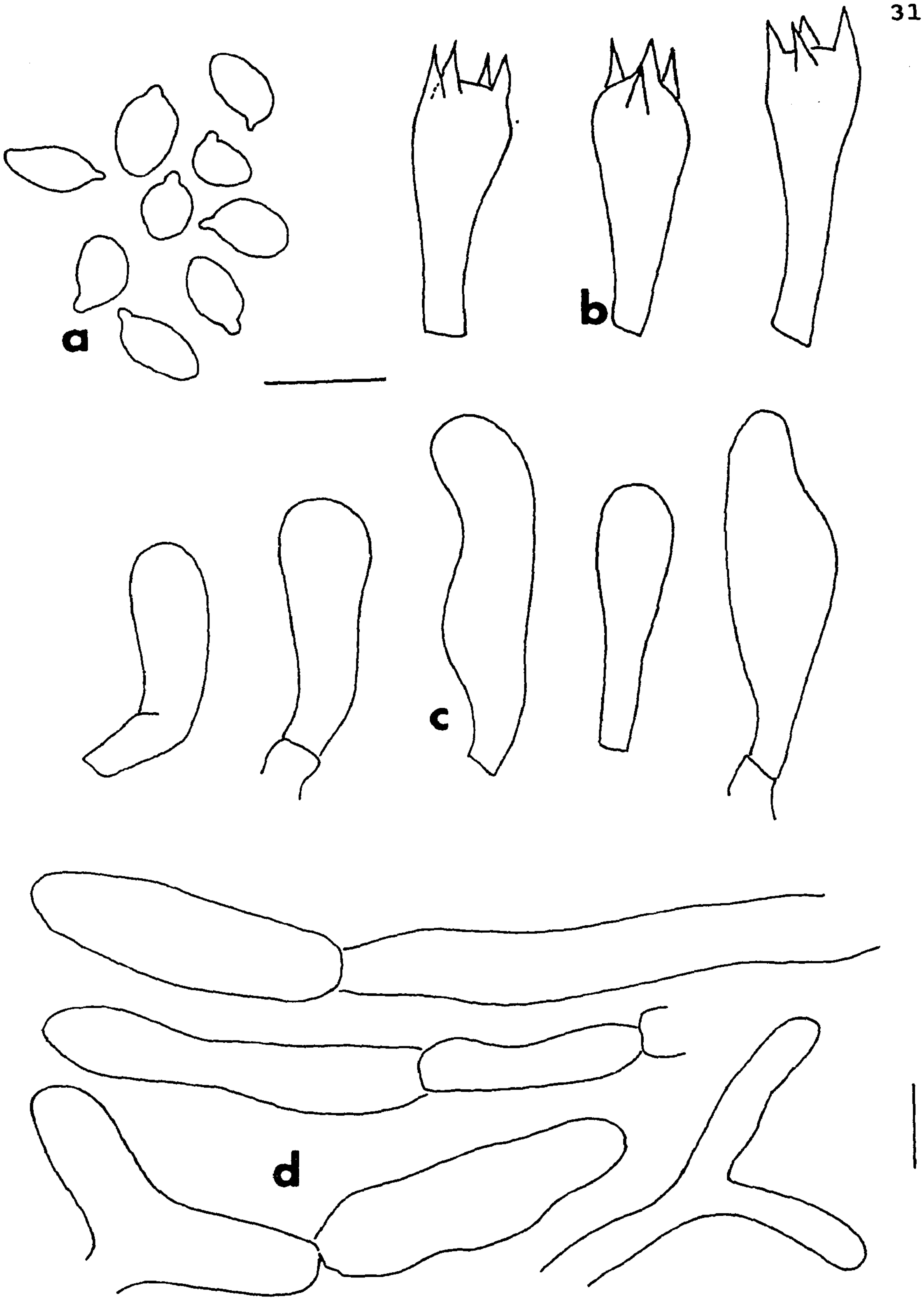
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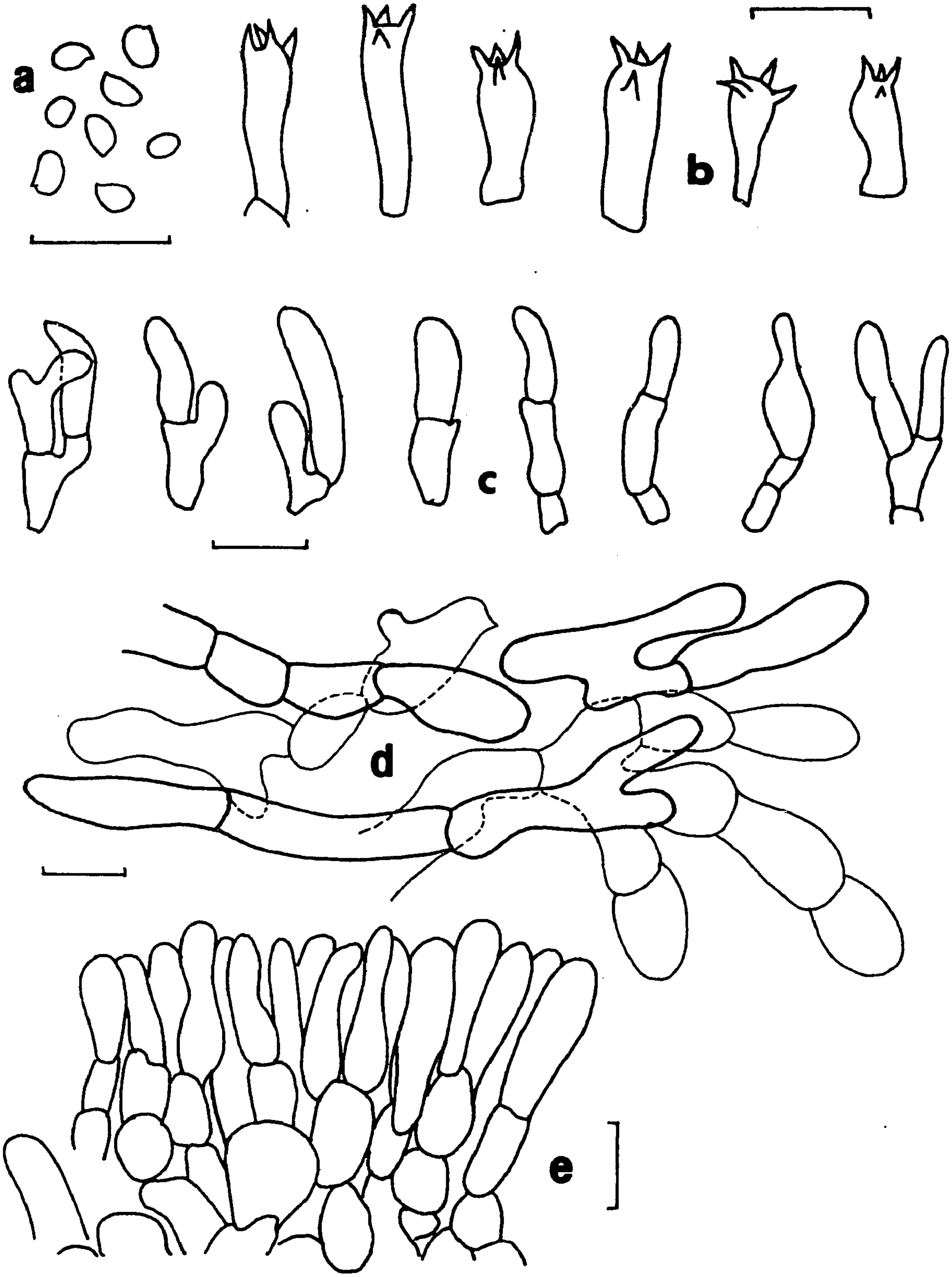
FIG. 53. Lepiota rubiginosoides (Franco-M. 710). Habit (1X).

FIGS. 54a-e. Line drawings of the microscopic features of *Lepiota rubiginosoides* (*Franco-M. 710*). a. Basidiospores. b. Basidia. c. Cheilocystidia. d. Subpileipellis. e. Suprapileipellis. Scale lines = 10 μm.


a
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APPENDIX I

List of Herbaria

The types and other collections examined during this work were received as loans or gifts from the following institutions [(abbreviations are from Holmgren et al. (1990)]:

BR	**MEISE:** Herbarium Nationale Plantentuin van Belgie, Jardin Botanique National de Belgique, Domein van Bouchout, B-1860 Meise, Belgium.
COL	**BOGOTA:** Herbario Nacional Colombiano, Instituto de Ciencias Naturales, Museo de Historia Natural, Universidad Nacional de Colombia, Apartado aereo 7495, Santafé de Bogotá, D. E. Colombia.
CUVC	**CALI:** Herbario, Departamento de Biología, Universidad del Valle, Apartado Aéreo 25360, Cali, Valle, Colombia.
F	**CHICAGO:** Herbarium, Botany Department, Field Museum of Natural History, Roosevelt Road at Lake Shore drive, Chicago, Illinois 600605-2496, USA.
FH	**CAMBRIDGE:** Farlow Reference Library and Herbarium of Cryptogamic Botany, Harvard University, Massachusetts 02138, USA.
HUA	**MEDELLIN:** Herbario, Centro de Investigaciones Ciencias Exactas y Naturales (CIEN), Universidad de Antioquia, Apartado Aereo 1226, Medellín, Antioquia, Colombia.
K	**KEW:** Herbarium, Royal Botanic Garden, Kew, Richmond, Surrey TW9 3AB, England, UK.
LPB	**LA PAZ:** Herbario Nacional de Bolivia, Correo Central Cajon Postal 10077, La Paz, Bolivia.
MICH	**ANN ARBOR:** Herbarium University of Michigan, North University Building, Ann Arbor, Michigan 48109-1057, USA.

NY	**NEW YORK:** Herbarium, New York Botanical Garden, Bronx, New York 10458-5126, USA.
NYS	**ALBANY:** Herbarium, Biological Survey, New York State Museum, Albany, New York 12230, USA.
PACA	**SAO LEOPOLDO:** Herbario Anchieta, Instituto Anchieta e Unisinos, Caixa Poastal 274, 93010 Sao Leopoldo, Rio Grande do Sul, Brasil.
PC	**PARIS:** Herbier, Laboratoire de Cryptogamie, Museum National d'Histoire Naturelle, 12 rue Buffon, F-75005 Paris, France.
TENN	**KNOXVILLE:** Herbarium, Botany Department, University of Tennesse, Knoxville, Tennesse 37996-1100, USA.
XAL	**XALAPA:** Herbario, Instituto de Ecología, A. C., Apartado Postal 63, 91000 Xalapa, Veracruz, Mexico.

APPENDIX II

Neotropical species of *Lepiota* s.l.

Cystolepiota albogilva Singer
  Brazil.

Cystolepiota amazonica Singer
  Brazil.

Cystolepiota cinereofusca Singer
  Costa Rica.

Cystolepiota eriophora (Peck) Knudsen
  Lepiota eriophora Peck
  Lepiota echinella var. *eriophora* (Peck) J. Lange
  Guadaloupe and Venezuela.

Cystolepiota hemisclera (Berk. & Curtis) Pegler
  Agaricus hemisclerus Berk. & Curtis
  Lepiota hemisclera (Berk. & Curtis) Saccardo
  Martinique and Cuba.

Cystolepiota potassiovirens Singer
  Brazil

Lepiota abruptibulba Murrill
  Trinidad and Tobago

Lepiota albiceps Patouillard & Gaillard
  Venezuela

Lepiota alluvina (Peck) Morgan
  Trinidad

Lepiota armillarioides Dennis
  Trinidad

Lepiota azalearum (Murr.) Dennis
  Cortinellus azalearum Murrill
  Martinique and Trinidad

Lepiota bakeri Dennis
  Trinidad

Lepiota biornata (Berk. & Br.) Saccardo
  Trinidad

Lepiota callamba Patouillard & Lagerheim
Ecuador

Lepiota carminea Patouillard & Gaillard
Venezuela

Lepiota cigroensis Guzmán-Dávalos & Guzmán
México

Lepiota citriodora Dennis
Martinique and Trinidad

Lepiota citrophylla (Berk. & Br.) Saccardo
Agaricus citrophyllus (Berk. & Br.) Saccardo
Trinidad

Lepiota cultorum (Berk. & Curt.) Saccardo
Trinidad

Lepiota diffracta Patouillard & Gaillard
Venezuela

Lepiota epicharis (Berk. & Br.) Saccardo var. occidentalis Dennis
Martinique, Venezuela and México.

Lepiota erinana Dennis
Martinique, Trinidad and Venezuela.

Lepiota erythrosticta (Berk. & Br.) Saccardo
Agaricus erythrostictus Berk. & Br.
Martinique, Guadaloupe, Trinidad, New Guinea, Sri Lanka, and West Africa.

Lepiota flavidocana Pegler
Guadaloupe and Trinidad

Lepiota gomezii Singer
Costa Rica

Lepiota gracilis Peck
Trinidad

Lepiota griseorubescens Dennis
Martinique and Venezuela

Lepiota griseosticta Cifuentes & Guzmán
México

Lepiota guatopoensis Dennis
Martinique, Guadaloupe and Venezuela

Lepiota ianthinosquamosa Pegler
Martinique

Lepiota lactea Murrill
Lepiota micropholis (Berk. & Br.) Saccardo var. lactea (Murr.) Dennis
Martinique, Guadaloupe, Trinidad and Cuba.

Lepiota lilacea Bresadola
Venezuela

Lepiota lineata Pegler
Martinique, Trinidad and Venezuela

Lepiota lotharingiana Pegler
Martinique

Lepiota microcystidiata Guzmán-Dávalos & Guzmán
México

Lepiota minima (Berk.) Dennis
Hiatula minima Berk.
Leptomyces minimus (Berk.) Murrill
Trinidad, Santo Domingo

Lepiota montagnei (Kalchbr.) Saccardo var. congolensis Beeli
México

Lepiota mucrocystis Pegler
Lepiota biornata sensu Dennis
Dominica & Trinidad

Lepiota mucronata Guzmán-Dávalos & Guzmán
México

Lepiota multicolor Murrill
Trinidad

Lepiota murino-capitata Dennis
Venezuela

Lepiota nigropunctata Dennis
Trinidad, Costa Rica

Lepiota ochraceolamellata Dennis
Venezuela

Lepiota ochraceoaurantiaca Dennis
Trinidad

Lepiota parvispora Dennis
Venezuela

Lepiota phaeosticta Morgan
Lepiota micropholis sensu Baker & Dale
Martinique, Dominica, Trinidad and México.

Lepiota pseudoignicolor Dennis
Lepiota subgranulosa var. *majus* Dennis
Guadaloupe and Venezuela

Lepiota pseudoroseola Dennis
Dominica, Venezuela and México

Lepiota quinamana Dennis
Trinidad

Lepiota quintanaroensis Guzmán-Dávalos & Guzmán
México

Lepiota rimosa Murrill
Trinidad, Cuba and Costa Rica

Lepiota roseolamellata Dennis
Martinique and Trinidad

Lepiota rubrotincta (Peck) Peck
México and Trinidad

Lepiota serena (Fr.) Saccardo
Agaricus serenus Fr.
Pseudobaeospora serena (Fr.) Locq.
Leucoagaricus serenus (Fr.) Bon & Boiff.
Sericeomyces serenus (Fr.) Heinem.
Martinique

Lepiota sordescens (Berk. & Curt.) Saccardo
Trinidad and Cuba

Lepiota spiculata Pegler
Martinique

Lepiota subamanitiformis Dennis
Trinidad

Lepiota subclypeolaria (BerK. & Curt.) Saccardo
Agaricus subclypeolarius Berk. & Curtis
Martinique, Dominique, Trinidad and Cuba

Lepiota subcristata Murrill
Guadaloupe, Trinidad, Jamaica.

Lepiota subflavescens Murrill
Martinique and USA.

Lepiota subgranulosa Murrill
Martinique, Trinidad and México

Lepiota tepeitensis Murrill
Martinique and México

Lepiota termytomyces Guzmán-Dávalos & Guzmán
México

Lepiota tobagensis Dennis
Tobago

Lepiota volvatula Pegler
Martinique

Lepiota zamurensis Patouillard & Gaillard
Martinique, Trinidad, Venezuela.

Leucoagaricus hortensis (Murr.) Pegler
Lepiota americana sensu Baker & Dale
Trinidad

Leucocoprinus bakeri (Dennis) Singer
Lepiota bakeri Dennis
Venezuela

Leucocoprinus birnbaumii (Corda) Singer
Agaricus birnbaumii Corda
A. cepaestipes Sow. : Fr. var. *lutea* Bolt.: Secr.
A. flos-sulphuris Schizlein
A. luteus (Bolt. : Fr.) Secr.
A. cepaestipes var. *flos-sulphuris* (Schinizlein) Oudemans
Lepiota flammula (Alb. & Schw.) Gillet
L. lutea (Bolt.: Secr.) Godfrin
L. aurea Massee
L. pseudolicmophora Rea
L. coprinoides Beeli
Leucocoprinus luteus (Bolt.: Secr.) Locq.
L. flos-sulphuris (Schnizlein) Cejp.
Martinique, Trinidad, Tobago, Venezuela, Bermuda, México.

Leucocoprinus brebissonii (Godey) Locquin
Lepiota brebissonii Godey
Martinique

Leucocoprinus brunnescens (Peck) Pegler
Lepiota brunnescens Peck
Martinique

Leucocoprinus cepaestipes (Sow. : Fr.) Pat.
Agaricus cepaestipes Sow. : Fr.
A. continuus Berk.
A. rorulentus Panizzi
A. cheimonoceps (Berk. & Curtis)
A. oncopus Berk. & Br.
A. oenopus Berk. & Br.
A. adoreus Berk. & Br.
Lepiota cepaestipes (Sow.: Fr.) Kuntze
L. rorulenta (Panizzi) Barla
L. continua (Berk. & Br.) Saccardo
L. oenopus (Berk. & Br.) Saccardo
L. odorea (Berk. & Br.) Saccardo
L. cheimonoceps (Berk. & Br.) Saccardo
Mastocephalus cepaestipes (Sow.: Fr.) Kuntze
Hiatula cepaestipes (Sow.: Fr.) Heim. & Romanegsi
Martinique, Dominica, Antigua, Trinidad, Jamaica,
Bahamas, and México.

Leucocoprinus fragilissimus (Rav.) Pat.
Hiatula fragilissima Rav.
Agaricus licmophorus (Berk. & Br.) Saccardo
Mastocephalus licmophorus (Berk. & Br.) Saccardo
Agaricus fragilissimus (Rav.) P. Henn.
Lepiota fragilissima (Rav.) Morgan
Hiatula licmophora (Berk. & Br.) Petch.
Leucocoprinus licmophorus (Berk. & Br.) Pat.
Martinique

Leucocoprinus meleagris ([Sow.] S. F. Gray) Locq.
Agaricus meleagris ([Sow.] S. F. Gray) Pers.
Gymnopus meleagris ([Sow.]) S. F. Gray
Lepiota meleagris ([Sow.] S. F. Gray) Quél.
Hiatula meleagris ([Sow.] S. F. Gray) Singer
Martinique

Leucocoprinus squamulosus (Mont.) Pegler
Hiatula squamulosa Mont.
Dominique, French Guiana, Guyana and Cuba.

Leucocoprinus sulphurellus Pegler
Martinique, Guadaloupe.

Leucocoprinus tenellus Pegler
Martinique

Leucocoprinus venezuelanus Dennis
Martinique and Venezuela

Macrolepiota dolichaula (Berk. & Br.) Pegler & Rayner
Agaricus dolichaulus Berk. & Br.
A. beckleri Berk.
Lepiota dolichaula (Berk. & Br.) Saccardo
L. backleri (Berk.) Saccardo
Leucocoprinus dolichaulus (Berk. & Br.) Boedijn
México

Macrolepiota mastoidea (Fr.) Singer
Agaricus mastoideus Fr.
Lepiota mastoidea (Fr.) Kummer
L. umbonata (Schum.) Schroet.
Lepiotophyllum mastoideum (Fr.) Locq.
Leucocoprinus mastoideus (Fr.) Locq.

Rugosospora pseudorubiginosa (Cifuentes & Guzmán) Guzmán & Bandala
Lepiota rubuiginosa Cifuentes & Guzmán
Mexico and Colombia

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[The list of Neotropical species of Lepiota s. l. (Appendix II) is excluded from this Index]